









# **ILLINOIS BIOLOGICAL MONOGRAPHS**

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# THE SKULL OF AMIURUS

WITH EIGHT PLATES

BY  
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Contributions from the  
Zoological Laboratory of the University of Illinois  
under the direction of Henry B. Ward No. 135

**THESIS**

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## INTRODUCTION

The study of the development of the teleost skull has been confined for the most part to isolated stages and there have been very few papers dealing with the changes which take place in any one species. Parker's (1872) work on the development of the cranium of *Salmo* has remained the standard and has been supplemented by Gaupp (1902) and Schleip (1903). Winslow (1897) describes the chondrocranium of the trout, Ryder (1886) and Pollard (1895) the chondrocrania of some of the Siluroids, but none of these attempted to trace the formation of the bones and their relation to the cartilage, in the same way that Parker did. Swinnerton (1902) has described several stages in the development of the skull of *Gasterosteus*.

The skull of the adult teleost has been widely studied in a topographical way, but very few authors have analyzed the bones in terms of their developmental relations, so that a wide field is open for this line of investigation. Gouan (1770) gives a simple account of the bones of the cranium and naively states that although there are many bones in the cranium of the young fish, these fuse into several large bones in the adult, as in man. Many of the names in use in the terminology of the present time have come directly from Cuvier, but others have been introduced into the literature principally by Owen (1848), Huxley (1864), and Parker (1872). Except for a few scattered references to the cranium of *Silurus glanis*, *Clarias*, *Auchenaspis*, and the incomplete description of the cranium of the adult *Amiurus* by McMurrich (1884), the skull of the Siluroids has been neglected.

This study of *Amiurus* has been undertaken because of the low organization of the Siluroids and the primitive relation of certain parts of the skull. Many points of relationship with the ganoids have been found and a sounder basis for grouping the Siluroids with the Characinidae and the Cyprinidae, has been developed. Very early stages of the skull were not procurable, so that the following account is based upon the 8, 10, 20, 32 and 60 mm. stages, though earlier stages than the earliest of these may be described in a later paper. Most of the material was obtained from Wisconsin, though the 32 mm. stage was supplied by Professor J. S. Kingsley under whose direction the work was completed, and whom I take this opportunity to thank for the many helpful suggestions and facilities placed at my disposal. The adult specimens, obtained through the generosity of the Illinois Natural History Survey, came from the Illinois River.

## THE CHONDROCRANIUM OF THE 10 MM. LARVA

The description of the early chondrocranium of *Amiurus* is based upon the study of a group of specimens from 8 to 10 mm. in length. Earlier stages than the 8 mm. larva were not procurable. From one series of transverse sections of a 10 mm. larva of *A. nebulosus* (catus), a wax model of the entire cranium and the visceral arches was made by Born's method of reconstruction. The description of this is supplemented by a careful microscopical examination of several other specimens.

The cranium is elongate and not as depressed as it is in the adult animal. There is no roof of cartilage or of bone above the brain at this stage, although a transverse bar between the alisphenoid cartilages of the two sides divides the large space into an anterior and a posterior fontanelle (Fig. 2). The anterior of these is the smaller and is limited to the region above the forebrain and the olfactory region. The posterior fontanelle is very large and extends posteriorly between the dorsal margins of the otic capsules, its posterior margin is formed by the occipital arch.

The floor of the cranium is fenestrated by the large oval fenestra hypophyseos (*f.h.*), which extends from the anterior end of the parachordal plate (*pch*) to the posterior end of the ethmoid plate (*eth*), the trabeculae cranii (*tr*) forming its lateral margins. The parachordal plate is solid posteriorly and is grooved for the reception of the sacculi of the inner ears. On either side and above the parachordal plate the otic capsules are situated and the only foramina in the wall of the cranium in this region are those for the passage to the exterior of the glossopharyngeal (Fig. 1, IX) and vagus nerves (X), nothing comparable to the posterior basicranial fenestra and the basicapsular fenestrae of *Salmo* (Parker, 1872; Gaupp, 1906) being observed. The cavum of the labyrinth opens widely into the cavum cranii. The alisphenoid cartilage, extending dorsally and anteriorly from the anterior end of the otic capsule, forms the dorsal margin of a large foramen in the cranial wall, through which the optic, oculomotor, abducens, trigeminal and facialis nerves issue (Figs. 1, 2). The nerves penetrate the connective tissue membrane which extends across the fenestra from the alisphenoid cartilage to the trabecula cranii (Fig. 14). The detailed descriptions of the various regions of the cranium and the comparisons with the chondrocranial parts of other forms follows.

*The ethmoid region.* At the 10 mm. stage in the development of the ethmoid region, the dorsal surface of the cartilage forms a trough, the sides of which are formed by dorsal projections near the lateral edges of the plate; the floor is formed by the ethmoid plate itself (Fig. 2). The olfactory lobes

lie in this trough and are roofed by membrane which extends between the two lateral projections and is attached dorsally to the integument. The olfactory foramen, which is very large at this stage, occupies the anterior half of the lateral wall of this region and the olfactory lobe protrudes through this foramen (Fig. 1). A short olfactory tract extends from the lateral part of the lobe to the olfactory bulb which lies just lateral to it. The ethmoid plate extends laterally beyond these walls (Fig. 30) and forms the floor, called by Gaupp (1906) the *solum nasi* in *Salmo*, of the nasal fossa of each side (Fig. 2). The anterior end of the plate projects as two massive cartilaginous processes, the ethmoid cornua (Fig. 2). Just behind these a transverse ridge in the middle of the plate forms the anterior end of the *cavum cranii* and marks the anterior extent of the olfactory lobes. The ventral surface of the ethmoid plate is slightly concave (Fig. 30). At the posterior end of the ethmoid region, the anterior ends of the fused trabeculae and alisphenoid cartilages fuse with the side walls and floor of the trough and the floor forms the anterior margin of the *fenestra hypophyseos* (Fig. 2). Each lateral wall of the ethmoid region is produced laterally into an ectethmoid process, which projects abruptly from the external face of the cranial wall and the ventral face of which forms the articular surface for the palatine cartilage (Fig. 1). The anterior face of the process is concave near its ventral margin: the ophthalmic superficialis ramus of the trigeminus passes obliquely through the dorsal margin. The posterior face of the process is fused medially to the anterior dorsal margin of the alisphenoid cartilage. The ventral part of this fused region is separated from the trabecula by a small foramen, behind the ectethmoid process, the orbital foramen (Fig. 1). This foramen is the posterior limit of the ethmoid region or wall. As yet there is no internasal septum between the olfactory lobes of the two sides. The oblique eye muscles have no relation to the ventral surface of the ethmoid plate as they have in *Salmo* (Gaupp, 1906), but are attached to the ventral margin of the orbital foramen posterior to the ectethmoid process.

Sagemehl (1885) discussed the morphology and development of the olfactory region in the different families of teleosts. He recognized three different degrees of relationship between the olfactory organ, the bulbous olfactorius, and the brain. In the first and most primitive relation which he described as the Cyclostome type, the bulbous lies between the brain and the organ, within the *cavum cranii*, closely fused to each. With subsequent development a long tractus olfactorius is spun out between them, and the bulbous remains applied to the olfactory organ. He called this the Selachian type, as it is most common in this group. It is also found in the Cyprinoids, Siluroids, Mormyrids, and Gadids among the teleosts. In these families the tractus always lies within a canal directly continuous with the *cavum cranii*.

In other teleost families, as represented by *Salmo*, a membranous inter-orbital septum is developed between the orbits, on the dorsal surface of the

trabecula communis. This septum, by growth backward and dorsally, limits the anterior extent of the cavum cranii. The bulbus olfactorius, which in the larva of one of these forms, has the primitive cyclostome relation, is carried posteriorly by the interorbital septum, so that it becomes enclosed within the cavum cranii. The bulbus retains its connexion with the olfactory organ by a long slender olfactory nerve which passes unenclosed across the orbit between the anterior end of the cavum wall and the ectethmoid process. Sagemehl recognizes this condition as the teleost type of olfactory development. It is also interesting to note that in the Characinidae (Sagemehl 1885), *Citharinus* is very close to the selachian type and *Macrodon* has the teleostean relation of parts. Other members of this family present greater or lesser degrees of relationship to the two types. The olfactory region at this stage of development in *Amiurus*, according to this view, has just reached the cyclostome stage.

*The orbital region.* Each lateral wall in the orbital region of the 10 mm. *Amiurus* is formed by a ventral trabecular and a dorsal alisphenoid cartilage, between which, the optic, oculomotor, most of the trigeminal, the abducens and the facialis nerves pass outward (Figs. 1, 2). In front of the opticus these two cartilages meet and form a solid wall for a short distance, its continuity being broken by the orbital foramen, dorsal to which the alisphenoid is fused to the posterior face of the ectethmoid process. Posteriorly the alisphenoid cartilage is fused to the anterior face of the otic capsule. A connective tissue membranous wall connects the ventral margin of the alisphenoid cartilage with that of the trabecula and it is through this membrane that the above mentioned nerves pass (Fig. 14).

The ramus oticus of the facialis nerve passes ventro-dorsally through the alisphenoid cartilage, just anterior to its union with the otic capsule. At about the middle of the cartilage are two small foramina, the more ventral for the ramus ophthalmicus superficialis of the trigeminus and the more dorsal for the ophthalmicus superficialis of the facialis (Figs. 1, 2). After its exit from the cranium and its passage through the orbit, the ophthalmic branch of the trigeminus passes through the orbitonasal foramen of the ectethmoid process, mentioned above, while the ophthalmic branch of the facialis passes around the lateral margin of the process.

A cartilage bar, the epiphysial bar, described by Sagemehl (1885) in the adult Characinidae and Cyprinidae, and by Pollard (1895) in the Siluridae, extends across the dorsal surface of the forebrain just posterior to the ectethmoid processes and is fused at each end to the anterior dorsal ends of the alisphenoid cartilages. There is no other trace of a cranial roof in this region at this stage.

The alisphenoid cartilage was described by Sewertzoff (1897) in the larval *Acanthias* as a large cartilage lying lateral to the fore- and mid-brains and connected secondarily with the anterior parachordalia. Later it fuses behind with

the anterior margin of the otic capsule and below with the posterior end of the trabeculae cranii thus enclosing the optic, oculomotor, trigeminus and facialis nerves. It grows anteriorly to the ectethmoid process, an independent cartilage, and fuses with it. Dorso-medially it grows toward the middle line and unites with its fellow of the opposite side to form the solid cranial roof. Except for its ventro-posterior relations, the alisphenoid of *Acanthias* can be compared to that of *Amiurus*. In both, these cartilages form the anterior and dorsal margins of the foramina for the nerves mentioned above, and extend across the dorsal part of the orbit. There is no cartilaginous roof in the chondrocranium of *Amiurus* with the exception of the epiphysial bar, which may be a remnant of such a condition. The notch at the anterior margin of the optic fenestra of *Acanthias* is suggestive of the orbital foramen of *Amiurus*.

Parker (1882) recognized three cartilaginous parts in the lateral wall of the orbital region of the chondrocranium of *Acipenser ruthenus*: a posterior alisphenoidal part, lateral to the parachordal plate; an anterior orbitosphenoidal part; and a dorsal supraorbital part, which fuses with its fellow of the opposite side to form the cranial roof. The orbitosphenoidal part is pierced by the optic nerve and the alisphenoidal part by the trigeminus and the facialis. This is more like the adult *Acanthias* cranium than it is like the cranium of the developing *Amiurus*.

In the chondrocranium of *Lepidosteus osseus* (Parker, 1882), the alisphenoid cartilage curves anteriorly above the nerves, from the anterior edge of the otic capsules. It is a thin flat bar and forms the lateral margin of the almost circular fontanelle in the cranial roof. Ventro-anteriorly it unites with the anterior ends of the trabeculae at the anterior end of the orbit, as in *Amiurus*. Medially and anteriorly it fuses with its fellow, above the fore-brain, forming a solid cartilaginous tegmen cranii, the remnant of which as above, may be represented by the epiphysial bar of *Amiurus*.

Concerning this region in the *Polypterus* chondrocranium, Budgett (1900) says: "The lateral walls of the cranium extend forward from the auditory region on either side of the alisphenoid region as continuous vertical plates of cartilage, somewhat dumb-bell shaped in section and perforated by foramina for the III, V, and VII nerves in the thinner middle portion. In the sphenethmoid region there is a large lateral fontanelle closed only by membrane through which passes the optic nerve, while above and below this membranous portion there pass the thickened upper and lower cartilaginous borders of the cranial wall, connecting on either side the ethmoid region with the posterior region of the cranium."

Dorsally the alisphenoid cartilages of the two sides in *Polypterus* are connected with each other by a transverse cartilaginous bridge, which is placed further back in the roof than the epiphysial bar in the cranium of *Amiurus*. The general relations of the alisphenoid cartilage to the cranial nerves in this region are much the same as in the developing *Acanthias*, and are closer to

that condition than to the condition found in the chondrocranium of *Amiurus*. The epiphysial bar, which is found again among the Teleosts in *Gasterosteus* (Swinnerton 1902), the Characinidae (Sagemehl 1885), the Cyprinidae (Sagemehl 1891) and other Siluridae (Pollard 1895), is the striking feature of a comparison between these two forms, as *Polypterus* is specialized in so many other features, that it differs from even the majority of the ganoids and has been mentioned as representing the ancestral stage of the Stegocephali.

In *Gymnarchus niloticus* (Assheton, 1907) the early chondrocranium of which has been very briefly described from Budgett's collections and notes, there is a long slit-like foramen in the wall of the orbit just anterior to the otic capsule and a smaller anterior foramen separated from this for the passage of the opticus. There is also a transverse bar similar to the epiphysial bar of *Amiurus* and *Polypterus*, connected however with the anterior ethmoidal roof by a median longitudinal bar of cartilage, which divides the anterior fontanelle into two parts. This may be the representative of a group in which the reduction from the solid cartilaginous roof of the lower ganoids is taking place, a continuation of which would produce the condition found in *Polypterus* and *Amiurus*.

In *Salmo salar* (Parker 1873; Gaupp 1906) a cartilaginous bar extends on each side of the cranium above the orbit, from the anterior end of the otic capsule to the posterior margin of the tegmen cranii, which extends back as far as the middle of the orbit. Posteriorly, between this bar and the otic capsule, the branches of the facialis and the jugular vein pass through separate foramina in the cartilage. The bar itself (called by Gaupp the taenia marginalis) extends anteriorly above the trigeminus and does not enclose any of its branches. Here, as in *Amiurus*, the large fenestra left in the wall between this cartilage and the trabeculae cranii is closed by membrane, through which the nerves issuing from the cranium pass. In *Amiurus*, as we have seen, both the fifth and seventh nerves issue through this membrane and with them the external carotid. In *Salmo*, as in *Acanthias*, these two nerves are separated from each other by a bar of cartilage, thus showing a nearer degree of relationship to the Selachian than to the Siluroid condition. The closer resemblance of *Salmo* to *Acanthias* is again evidenced by the presence of a well-developed tegmen cranii, not found in *Amiurus*.

In *Ceratodus* and the *Urodeles* the alisphenoid cartilage is fused ventrally with the trabecula during the first stages of development and later unites with the ethmoid and otic regions. As in the Ganoids and Teleosts, its anterior end and the trabecula enclose the optic nerve. Since the posterior ends of these cartilages enclose the trigeminus and the facialis, there is no question as to their homology with the alisphenoid and trabecular cartilages of these groups. Gaupp (1906) calls the former the crista trabeculae, thus adding to the confusion of names.

This same author claims that the cartilaginous bar, which I, following Sewertzoff, have called the alisphenoid cartilage, is not homologous with the alisphenoid cartilage of the Mammalia and therefore cannot be so named. He says that the ala temporalis in the mammalian cranium is a new formation, homologous with the process basiptyergoideus of the Lacertilian cranium, which arises from the procartilage cells around the anterior end of the palatopterygoid cartilage.

On comparison with the alisphenoid of mammals this homology falls to the ground if the relations of nerve and cartilage are used as the criteria for homologies of the chondrocranial parts. Throughout all of the lower Gnathostome groups the posterior end of this cartilage is connected with the development of the foramina for the passage of the branches of the trigeminus, but when such a cartilage appears in the mammals, the above associations are discounted and the cartilage is compared to an outside formation. In denying the homology, Gaupp takes this question into consideration, but maintains that the nerve relations are secondary and that nerves go through the ala temporalis because it replaces the original wall of this region. Assuming this to be the case, he states that anybody who relies upon the passage of nerves for their criteria of homology of cartilaginous parts is sure to err (1902). It is a settled fact, however, that are nerves constant throughout the vertebrate series and that they precede the cartilage in both ontogeny and phylogeny. Therefore, any homology which is made with these as a basis is sure to have a landmark which varies less than the parts of any other organic system, such as the blood vessels or muscles.

The trabeculae cranii are flat and acute on both inner and outer edges, becoming narrower anteriorly before uniting with the alisphenoid cartilages. Their posterior ends are fused with the anterior parachordalia and with them form the lateral margins of the fenestra hypophyseos and the fenestra basiscranii anterior (Figs. 2, 14). The anterior ends are fused to each other median to their union with the alisphenoid cartilages and form the posterior margin of the ethmoid plate which has been discussed. There is no trabecula communis such as occurs in *Salmo*, the cranium being distinctly platybasic. An internal carotid artery approaches the trabecula of its side ventrally, and enters the cranial cavity through the inner edge in about the middle region of the orbit (Fig. 2), and proceeds anteriorly in the membranous wall of the orbit. Each artery sends a branch along the dorsal surface of the optic nerve and then unites lateral to the cerebral hemispheres with an internal branch from the external carotid.

The rectus eye muscles and a ligament to the pterygoid cartilage are attached to the lateral surface of each trabecula in the posterior part of the orbit. There is no trace of a myodome in this or the later stages. The oblique eye muscles are inserted on the trabeculae below the orbital foramen.



The fenestra hypophyseos and the fenestra basicranii anterior are closed by a sheet of fibrous connective tissue which stretches between the trabeculae (Fig. 14) and extends anteriorly below the ethmoid plate and posteriorly below the parachordal plate. It is not intimately connected with the cartilage of any of these parts.

In a 19 mm. larva of *Amia*, the rectus eye muscles are inserted in a space between the brain and the trabeculae, including some connective tissue with them. In the adult *Amia* in this region there is a canal separated from the *cavum cranii* by the prootic ossification. The trabeculae are wider in *Amia* than they are in *Amiurus* and form a trabecula communis before fusing with the ethmoid plate. In *Amia* each internal carotid artery passes through the trabecula on its medial side. The artery gives off a branch above the optic nerve in *Amia* as it does in *Amiurus*. The fenestra hypophyseos in *Amia* is even smaller than in the known higher teleosts. In the cranial wall, anterior to the otic capsule, the fifth and seventh nerves are separated by a bar of cartilage between the trabecula and the otic capsule, as in the Selachians and the Salmonidae, differing in this respect from *Amiurus*.

The oblique eye muscles in a 19 mm. *Amia* are inserted in a foramen in the wall of the cranium between the ectethmoid process and the optic foramen, comparable to the orbital foramen of *Amiurus*. In *Amia* this foramen continues anteriorly with a groove on the dorso-lateral surface of the ethmoid plate. Beyond the eye-muscle insertion, the olfactory tractus continues along the anterior part of the same groove. In *Amiurus* this groove is lacking and the eye muscles do not enter the foramen. There is, however, a concavity on the anterior face of the ectethmoid process which, if continued through to the posterior, would end at the anterior margin of the orbital foramen and may have some significance in comparisons with the anterior continuation of the foramen in *Amia*. The cartilage of the ethmoid floor in this region between the anterior parts of the orbits, is thicker in *Amia* than it is in *Amiurus*.

In the *Acanthias* larva (Sewertzoff, 1897), the trabeculae develop as paired independent cartilages at right angles and ventral to the anterior ends of the parachordals, eventually becoming fused with their ventral faces. They grow forward on either side of the hypophysial region of the brain and fuse anteriorly as a trabecula communis plate. As the flexure of the neural parts disappears, the trabeculae become horizontal in position, except in that immediate region where they are attached to the parachordal plate. Unlike the trabeculae in *Amiurus*, the Selachian trabeculae later form a solid floor in the cranium. The cartilaginous connexion between the alisphenoid and trabecular cartilages is far more extensive in the later *Acanthias* than it ever is in *Amiurus*. The condition of the cranial floor of *Acipenser* (Parker, 1882a), is the same as that of *Acanthias*, although the fenestra hypophyseos may persist for a longer time. In the early *Lepidosteus* cranium (Parker, 1882b) there is a large fenestra hypophyseos which later becomes closed by the growth medially of

the trabeculae. There is a large fenestra hypophyseos in the chondrocranium of the larval *Polypterus* (Budgett, 1907) which, from its ellipsoidal shape, is comparable to that of *Amiurus*. In none of these, however, have the relation of the internal carotid and trabecula been brought out. In all cases the nerves of the cranial series, from the second to the seventh, issue from the cranium above the trabeculae.

In *Salmo* (Parker, 1872; Gaupp, 1906) the trabeculae unite immediately anterior to the hypophysial region to form an elongated anteriorly extending trabecula communis, on the dorsal surface of which the membranous interorbital septum rises. The relation of the trabecula to the nerves is typical, but the trabeculae do not meet the alisphenoid cartilages in the medial wall of the orbit as in the *Selachians*, *Ganoids*, and *Amiurus*. Further comparisons of the relations of the trabeculae in other groups than the fishes are made by Parker and Bettany (1877), and Gaupp (1906).

*The otic region.* The otic capsules at this stage are two large cartilaginous masses forming the sides of the posterior region of the cavum cranii (Figs. 1, 2). Ventrally, they are fused with the basal plate of the posterior cranial floor, from the posterior ends of the trabeculae to the occipital arch, and there is no gap (basicapsular fenestra, Parker, in *Salmo*) between each capsule and the basal plate. Posteriorly there is no line of division between the occipital arch and the posterior boundary of the otic capsules. Anteriorly the cartilage surrounding each auditory mass is confluent with the posterior end of the alisphenoid cartilage. The dorsal medial margins, at this stage, do not meet above the hind-brain to form a cartilaginous synotic tectum as is found in other teleosts (Fig. 2).

The vagus nerve passes obliquely between the otic capsule and the ventral end of the occipital arch, latero-dorsal to the parachordal plate. The glossopharyngeal nerve has a smaller and more anterior foramen in the floor of the otic capsule and is separated from the foramen of the vagus by a small bar of cartilage.

The cavum of the otic capsule is fully open to the cavum cranii, except at the extreme anterior end where there is a small medial wall, bounding the anterior part of the anterior semicircular canal. The cavum within the capsule is divided by three septa semicircularia into the cartilaginous labyrinth containing the membranous semicircular canals. The septum semicircularis anterior, as in the adult (Fig. 7), is a short bar of cartilage extending from the anterior wall of the capsule posteriorly to the midventral surface of the roof, parallel to the long axis of the body. From its dorsal connexion with the utriculus, the anterior membranous semicircular canal passes above this septum into the anterior part of the capsule. The septum semicircularis laterale is situated at right angles to the anterior septum between the roof and the floor of the capsule, but nearer to the posterior than to the anterior septum. The anterior end of

the membranous lateral semicircular canal and the ventral end of the anterior enter the cavum cranii anterior to this septum laterale. The posterior end of the membranous lateral semicircular canal and the ventral end of the posterior, enter posterior to it. The septum semicircularis posterius lies in about the same horizontal plane as the anterior and makes an angle of about 120 degrees with the ventral surface of the roof of the capsule. The posterior end of this septum is continued as a medial wall between the cavum of the posterior membranous semicircular canal and the cavum cranii. The dorsal end of this canal passes posteriorly above this septum. The fenestrae above both the anterior and posterior septa are much smaller than the fenestrae anterior and posterior to the lateral septum.

After leaving the ganglionic mass of the facialis, the ramus lateralis accessorius of this nerve proceeds dorsally and curves around the anterior end of the roof of the capsule and thence along the dorsal surface of the cartilage, above the occipital arch to the body musculature. In all this distance the nerve is unenclosed by cartilage, nor is there any indication of ossification around it. It is accompanied by a branch of the internal jugular which descends and fuses with the postcardinal vein in the region of the second neural arch.

The hyomandibular cartilage articulates with the external surface of the ventro-lateral wall of the anterior and lateral semicircular canals (Figs. 1, 2). This articulation extends from the ventro-anterior edge of the capsule just above the posterior margin of the foramen for the facialis nerve, posteriorly in an obliquely dorsal direction toward the lateral edge of the roof of the capsule. The articular surface is very small in comparison with the longitudinal extent of the capsule and at this stage there is no projecting shelf for this articulation. In a nine day *Ictalurus albidus* chondrocranium (Ryder, 1886), the hyomandibular articulation differs from that in *Amiurus*, the anterior end being more dorsal than the posterior and, in addition, the surface is smaller and is overlapped by a process from the anterior margin of the capsule, suggestive of the pterotic ridge of *Polypterus* (Budgett) in the same region. The hyomandibular articulation of other teleosts and some of the ganoids is in nearly the same plane and region as in *Amiurus*, this scheme of articulation appearing to be typical for these groups.

The otic capsule of the *Amiurus* type is apparently derived from a primitive condition represented by the Cyclostomes (Parker and Sewertzoff) and found in the larval *Acanthias* as well. In these forms the otic capsules are fused, ventrally, to the basal plate and the cavum of each communicates with the cavum cranii by a large foramen through which the seventh and eighth cranial nerves enter the capsule. The ninth and tenth nerves leave the cranium posterior to the capsule in the Cyclostomes, but are in the same relative position in the larval *Acanthias* as in *Amiurus*. In *Amiurus* (p. 13) these leave by separate foramina, the tenth between the otic capsule and the occipital arch, the ninth a little anterior. A description of the septa semicir-

cularia of the Cyclostomes is lacking, so a comparison with the inner surface of the capsules cannot be made. However the structure of the ears in these forms is so different from that of the Gnathostomes, that detailed comparisons would have little value here.

In the larval *Acanthias* the fenestra of communication between the cavum cranii and the cavum labyrinthii is as wide as it is in *Amiurus*, but a wall is beginning to grow from the line between otic capsule and basal plate, which will eventually separate the two cavi. Sagemehl, from his comparative morphological study of the crania of the teleosts, says that their condition in this region is derived from the constant fenestration of the foramen for the auditory nerve, rather than from the Cyclostome condition. The evidence given above of the presence of a wide fenestra in the larval *Acanthias* is against his view and in favor of the derivation of the condition in the teleosts from an ancestor with a wide fenestra.

The ninth and tenth nerves leave the cranium by separate foramina in *Acanthias* just as they do in *Amiurus*, as stated above. The synotic tectum in *Acanthias* is formed very early by the growth of the median margins of the otic capsules, a condition not reached by *Amiurus* until very late in the larval period and then only for a short distance anteriorly.

The relation of the capsules to the basal plate and to the cavum cranii of *Lepidosteus osseus* (Parker, 1882), is much the same as in *Amiurus* except for the large fenestra in the ventral floor of each capsule. There is no wall between the cavum cranii and that part of the capsule containing the inner ear. A detailed description of the septal relations is lacking.

Part for part, the otic capsule of the larval *Salmo* as described by Gaupp (1906) is nearer to the condition of *Amiurus* than any other that has as yet been described. Except for the precocity in the growth of *Amiurus* they can be said to be identical in all their relations, if the presence of the basicapsular fenestra in the floor of the capsule be left out of consideration. There is the same relation of cavum of the labyrinth to cavum cranii and the same number of septa semicircularia are present and have the same relation to the membranous labyrinth in both forms. The relations of the ninth and tenth nerves are homologous in both cases. Externally the hyomandibular articular surface is about in the same region in both. The synotic tectum of *Salmo* is very well developed as compared with that region of *Amiurus*. Except for the inclusion of the branches of the facialis between it and the alisphenoid cartilage in *Salmo*, the anterior margins of the capsules are homologous, although the processus postorbitalis is more pronounced in *Salmo* than in *Amiurus*. From these comparisons it may be observed that *Amiurus* has an otic capsule which, except for several minor differences, is typical of the teleostean condition.

*The parachordal region.* Authors describing the origin of the chondrocranium in the teleosts have remarked that the basal plate of the older larva

arises from paired cartilaginous masses lying lateral to the notochord. Stöhr (1882) differentiated each of these masses into an anterior and a posterior part, the anterior lying medial to the otic capsules, and the posterior behind the exit of the vagus nerve from the cranium. The parachordal masses, as these cartilages are called, eventually fuse, partially at least, with each other around the notochord, anteriorly with the posterior ends of the trabeculae, laterally with the otic capsules, and posteriorly form the base of the occipital region. Concerning the parachordals in a general way, Parker and Bettany (1877; p. 311) say: "When the parachordals unite in the region where the notochord still persists, it is by growth of the cartilage over and under it. The bridge beneath the notochord is very marked and becomes thick; the cartilage is thinner above, and often nonexistent for a long time, so that the notochord lies in a groove on the basilar plate constituted by the union of the parachordalia. In many cases where a basicranial fontanelle exists, the cartilages do not approach one another again, and the fontanelle is only closed by a bony growth. . . . The whole of the cranial notochord is gradually aborted in most instances, and its place is occupied by cartilage; but in various forms a remnant is left as a slender string, embedded in the basioccipital bone or cartilage."

In the chondrocranium of the 10 mm. *Amiurus*, the parachordalia have already passed through the early stages of development and are partially fused with each other, with the trabeculae, and the otic capsules, forming the base of the occipital region (Fig. 21).

Terry (1917) has recently worked over the literature on the parachordal region of the mammals and concludes that the parachordals may arise in three ways: from a hypochordal center of chondrification; from a pair of bilaterally placed masses; and by growth and fusion of the apposed ends of the lateral occipital arches. In the 10 mm. cat, the notochord enters the occipital region between two laterally lying parachordal cartilages, dorsal to a mesenchymal sheet which connects them. This sheet later becomes chondrified in connexion with the parachordals, forming thus an hypochordal bridge of cartilage. This agrees with the statement quoted from Parker and Bettany, but cannot be applied as a rule for the development of the basal plate of the teleost chondrocranium, as the condition in *Amiurus* shows.

The concavity marking the anterior extent of the notochord on the ventral surface of the plate is continued anteriorly beyond the tip of the notochord as far as the margin of the fenestra basicranii anterior. The anterior end of the notochord does not project into fenestra basicranii posterior, for such is absent in *Amiurus*. There is no fenestra between the parachordal and the otic capsule corresponding to the basicapsular fenestra of *Salmo*.

The sacculi of the inner ears have invaded the cartilage of the basal plate to such an extent that they have replaced most of it (Fig. 8). The grooves on the dorsal surface of the plate containing them extend from below the base

of the lateral septum semicircularis to the posterior end of the cranium, lateral to the notochord. The sacculi communicate with each other across the anterior ends of these grooves, above the tip of the notochord, by a transverse canal sinus impar (ductus endolymphaticus, Wright, 1884), from the posterior wall of which the sinus impar of the Weberian apparatus projects. This sinus impar lies along the mid-dorsal surface of the cavum floor and is separated from the laterally situated sacculi by a membranous V-shaped wall, the apex of which is attached to the dorsal surface of the notochord (Figs. 17, 21). It is separated from the cavum cranii by a membranous roof which continues laterally as the roof of the saccular recesses and is attached to the cranial wall at the junction of otic capsule and parachordal cartilages. Posteriorly, the membranous roof over the saccular cavities is replaced by cartilage which is continuous medially with the ventral walls of the cavum sinus imparis and laterally adjoins the otic capsule. The ventral floor of each recessus sacculi is very thin (Fig. 8), but the posterior wall which marks the posterior extent of the parachordal plate is thick dorso-ventrally (Fig. 21). The dorso-lateral surface of this posterior part of the parachordal plate is separated from the ventral end of the occipital arch posterior to the otic capsule (Fig. 17), and through this space the sinus impar communicates with the Weberian ossicles contained in the saccus paravertebralis. The first post-vagal nerve or hypoglossus passes out through this space, but does not touch the cartilage of the posterior end of the parachordal plate which has narrowed considerably in this region.

The relations of the inner ear to the cranial floor have been described by several investigators in those forms having a Weberian apparatus, but the descriptions have been confined to adult conditions. In a later paper, I hope to follow the developmental relations of the inner ear to the parachordals, if I am fortunate enough to obtain the proper stages.

There is no evidence of segmentation of the basal plate at this stage, such as is found at the posterior end of the parachordal plate of *Acanthias* (Sewertzoff, 1897). The distinct ridge of cartilage, called the 'Sattellehne,' is lacking in *Amiurus* because the trabeculae do not become attached to the ventral surface of the parachordalia, but lie in the same plane with them. Like the intercapsular floor of *Acanthias*, this region of *Amiurus* is solid, and, although in the early stages of *Acanthias* the notochord projects into the basi-cranial fenestra, it is later enclosed by cartilage as in *Amiurus*. The inner ear relations have nothing in common as regards the parachordal plate, because in the older *Acanthias* the cavum of the ear is shut off from the cavum cranii by a wall of cartilage.

As I was unable to find any statement concerning the later larval history of the parachordalia of *Amia*, I found it necessary to study a series of transverse sections through the head of a specimen 19 mm. long. I have referred

to the condition 'n the anterior region of the head of this same specimen earlier in this description.

The parachordalia do not extend beyond the anterior end of the notochord, but lie lateral to and separated from it by a space filled with a stroma of pro-cartilage cells. This space is comparable to the posterior basicranial fenestra which Gaupp has described for the 25 mm. *Salmo*, but which is lacking in the 10 mm. *Amiurus*. The parachordalia are triangular in cross-section and are fused latero-dorsally with the floor of the saccular cavity of the otic capsule. A sharp crest marks the line of division between the two, and from the dorsal edge of this crest a membrane extends to the roof of the cranium, separating the *cavum cranii* from the *cavum labyrinthii*. The sacculus lies on the capsular side of this membrane within the otic capsule, on a higher plane than the medial ends of the parachordals. As the parachordals extend posteriorly, they gradually come in contact with the lateral surfaces of the notochord, at first by a sharp edge which gradually becomes blunt and finally concave, as it comes into closer contact with the notochord. The parachordals of the two sides remain distinct from each other however, and I was unable to observe a region of fusion, either above or below the notochord. The glossopharyngeal nerve passes to the exterior through the *cavum labyrinthii* between the sacculus and the posterior semicircular canal. The passage of this nerve in *Amiurus* follows the same route between the sacculus and the semicircular canal, but the foramen lies between the dorso-lateral edge of the parachordal plate and the ventral margin of the capsule, rather than in the wall of the capsule proper as it does in *Amia*. The vagus nerve issues higher up in the wall than it does in *Amiurus* and instead of being ventral, is posterior to the otic capsule. The cartilage of the parachordals has a greater posterior extent in *Amia* than it has in *Amiurus*.

In a 25 mm. *Salmo*, as described by Gaupp, the parachordalia lie lateral to and close around the notochord, except at its anterior tip which projects freely into the posterior basicranial fenestra. This fenestra is cut off from the more anterior fenestra by a transverse bar of cartilage between the anterior ends of the parachordalia. The rectus eye muscles are inserted between the anterior ends of the parachordalia which form the lateral walls of an eye muscle canal in this region, the *cavum* of which is cut off from the *cavum cranii* by a membranous floor (See Gaupp, 1906, fig. 342). Commenting upon the parachordal relation Gaupp says: "Die Balkenenden verschmelzen mit den vorderen Parachordalia; die ursprüngliche Grenze liegt anfangs etwa in der Höhe der vordere Chordaspitze und entspricht dem (in dem Folge sich mehr verengernden) Uebergang der vorderen und hinteren basikranialen Fontanelle. Schliesslich tritt auch eine vordere und eine hintere Vereinigung zwischen dem Parachordale und dem inzwischen vergrossten periotische Knorpel ein."

As noted in the discussion of the otic region there is a fenestra between the parachordal cartilage and the otic capsule in *Salmo* which is not present in

Amiurus, and the ninth nerve issues through its posterior end. Whether the foramen for the passage of the ninth nerve in *Amia* and *Amiurus* is a remnant of this or not, it is hard to say without knowing the earlier history. The saccular relations are probably the same in *Salmo* as they are in *Amia*, as the Siluridae have a specialization not found in all of the teleosts, just as the eye muscle relations are peculiar in a certain large group with well-developed eyes.

The relations of the anterior end of the parachordals of *Amiurus* and of *Salmo* are homologous in that they lie between the otic capsules on either side of the notochord and are connected anteriorly with the trabeculae. Primitively they are alike, but specialization in one form in connexion with the ear and in the other with the eye have made detailed comparisons difficult.

*The occipital region.* As remarked above, the dorsal part of the occipital arch forms the posterior margin of the posterior fontanelle (Fig. 2). The occipital-otic capsule fusion takes place above the foramen for the vagus nerve, and behind it the ventral ends of the occipital arch are fused for a short distance to the parachordals (Fig. 21). Behind this region of fusion the anterior ends of the scaphoid processes project between the occipital arch and the parachordals. At this stage, the scaphoid process is a membranous plate connected posteriorly with the perichondrium of the cartilaginous scaphium (Fig. 13).

The first post-vagal nerve (Figs. 17, 35) leaves the vertebral canal between the anterior end of the scaphoid process and the ventral end of the occipital arch. This part of the arch is enclosed in a perichondrial ossification, even at this stage. The anterior margin of the foramen for the passage of the nerve is formed by the occipital arch-parachordal fusion. The cartilage of the parachordals does not extend posterior to this immediate region, and the diameter of the notochord is much larger than it was intercranially (compare Figs. 8 and 17). The elastica interna and externa are very distinct from each other in this part of the notochord.

On the median dorsal surface of the notochord there is a thickened mass of connective tissue, the endorhachis, which forms a floor for the support of the spinal cord (Fig. 13). This floor is supported laterally by connexion with the ventral ends of the occipital arch. In this manner the space between the occipital arch and the notochord is divided into three chambers, a dorsal unpaired one containing the spinal cord, and two lateroventral chambers, the lateral walls of which are formed by the scaphoid processes. The saccus paravertebralis lies external to each scaphoid process and contains the ossicles of the Weberian apparatus. The lateral chambers within the scaphoid processes are called the atria sinus imparis and are the posterior continuation of the sinus impar.

The scaphium (Fig. 13) at this stage, is a small piece of cartilage which articulates with the dorso-lateral surface of the notochord by a rounded end. It has all the appearances of a modified neurapophysis. Between its dorsal



end and the occipital arch there is a small triangular piece of cartilage, the claustrum of the Weberian apparatus. Sagemehl (1885) regarded this in the Characinidae as the first true neurapophysis, and maintained that the nerve which originally passed between the claustrum and the scaphium has been suppressed in those groups having a Weberian apparatus. The scaphium was homologized to the second neurapophysis.

The second pair of neurapophyses lie a short distance posterior to the scaphia and are separated from them by a pair of rather wide foramina through which the second pair of postvagal nerves issue (Figs. 12, 35). The ventral ends of these neurapophyses are concave and are closely applied to the notochord, in contradistinction to the rounded ends of the scaphia. Above the dorsal ends of this second pair of neurapophyses and the claustrum, the posterior end of the occipital arch has narrowed to a small process which is inserted into the anterior face of the third neural arch (Fig. 12). The posterior and ventral ends of this neural arch descend behind the second pair of neurapophyses, leaving a wide foramen in the wall on each side. The third post-vagal nerve (Fig. 35) passes out through this foramen, nearer to the second neurapophysis than to the third.

Briefly, the skeletal and nerve elements alternate with each other in this region, just as they do farther back in the body (Fig. 35). None of the post-vagal nerves are actually included within the cranium at this stage, as the dorsal and ventral parts of the occipital region have not as yet united posterior to the first pair. The dorsal surface of the occipital arch does not show any segmentation and ventrally it is continuous with the parachordalia posterior to the passage of the vagus nerve and the otic capsule (Fig. 21). The parachordal cartilages do not extend posteriorly beyond the passage of the first post-vagal nerve and there is no cartilage lateral to the notochord until the ventral ends of the third neural arch are reached.

There are four distinct muscle segments between the posterior end of the otic capsule and the ventral end of the third neural arch on each side (Fig. 35). The more anterior are dorsal and oblique to the posterior, which extend in under their ventral ends (Figs. 12, 13). The first myotome is very short and projects into the shallow temporal fossa, lateral to the dorsal half of the occipital arch (Fig. 12). The second starts ventral to the first, and lateral to the passage of the first postvagal nerve. It is separated from the cartilage of the occipital arch by a wide space filled with loose connective tissue. The third myotome comes in below the second, lateral to and above the second post-vagal nerve, and the fourth is lateral to the anterior projection of the neural arch of the third vertebra. Distinct myosepta are present between all of these segments.

All the post-vagal nerves have both dorsal and ventral roots, but the first is the only one in which the ganglion of the dorsal root lies within the cavum spinalis. The ganglia of the others all lie external and lateral to the side walls of

the neural arches. All except the first have very well developed dorsalis and lateralis rami and usually an additional dorsal sensory ramus which proceeds dorsally to the epidermis (Fig. 12). The ramus lateralis of the first post-vagal nerve (Fig. 17) descends obliquely to the muscles in the ventral wall of the body between the parts of the shoulder girdle, and in this way is comparable to the somatic hypoglossal nerve of the higher groups. The first two muscle segments have no visible innervation. The third and fourth muscle segments are innervated by the distinct rami dorsales of the second and third nerves. The rami laterales of these two nerves descend, as did the ramus lateralis of the first nerve, to the musculature between and around the developing shoulder girdle.

The work of Gegenbaur (1887), Sagemehl (1884, 1885, 1891), Froriep (1901), Stöhr (1882), Dohrn (1901), Sewertzoff (1895), Van Wijhe (1882), Fürbringer (1897), and others on the relation of the trunk and head in the occipital region has been reviewed by Gaupp (1906). He emphasizes the work of Fürbringer as a step in the right direction for the understanding of this question and I refer briefly to some of the points of interest in the researches of Fürbringer (1897).

According to this author, the crania of the Teleosts may be divided into two parts, and anterior paleocranium, ending with the vagus, and a part posterior to this, the neocranium. The neocranial condition arose from the assimilation of body segments and is represented in the occipital part of the cranium by skeletal segments and nerves. The primitive type of neocranium is termed the protometameric and is represented in the present day forms in the crania of the Selachians and the Amphibia. When more elements are assimilated the auximetameric condition is reached. This type of neocranium is found in the higher fishes and in the Amniotes. The distribution and occurrence of nerves posterior to the vagus are used by the author in his analysis of the types of neocrania in the different groups. The paleocranial nerves end with the vagus and the neocranial are those, which, before becoming included within the cranium, were of a free spinal type. These nerves so included are called the 'spino-occipital' nerves and are further divided into two categories; those enclosed in the protometameric neocranium are known as the 'occipitale' nerves and those in the auximetameric neocranium as the 'occipito-spinale' nerves. He explains the difference in number and appearance of these nerves in the different animal groups as the result of more or less assimilation of vertebrae and atrophy of somites. In his diagrammatic representations of the condition in the Selachians, the last 'occipitale' nerve is represented by the letter 'z' and the first of the 'occipito-spinale' nerves of the higher fishes and the Amniotes as 'a,' the homologue of the first free spinal nerve of the Selachians. Holocephala, Ganoids, Dipnoi, Teleosts, and Amniotes possess an occipital region of the auximetameric type. According to Fürbringer, different numbers of vertebrae and segments take part in the formation of this region,

so that the cranium does not end in the same place in all of these groups. The cranial-vertebral complex of the Amniotes includes three vertebrae and the hypoglossus nerve of this group is the result of the fusion of the three nerves corresponding to these three vertebrae. He says, that in a general way the auximetameric neocranium of the teleost agrees with the Amniotic condition.

The nerve formula for the occipital region of the Siluroids is b-0-4. According to this view, the first post-vagal nerve of *Amiurus* is an 'occipito-spinale' nerve and corresponds to the second free spinal nerve of the Selachians, which the Arabic numeral represents. Thus, there is one segment missing between the paleocranium of *Amiurus* and the auximetameric neocranium, and another between this and the first free spinal nerve. This method of reasoning is based on Sagemehl's hypothesis that in the Characinidae and the Siluridae, where the Weberian apparatus is developed, the claustrum represents the neurapophysis of a rudimentary vertebra, and that the nerve which originally came in between the claustrum and the scaphium is lost, together with the muscle segment. I do not regard the claustrum as a rudimentary vertebra, but as an intercalated cartilage, developed in connexion with the specialized Weberian ossicles. The scaphium may be the first true neurapophysis and a modified representative of this part of the first vertebra. I hope to get further evidence later for the exact somitic relations of these parts in younger larva than have yet been accessible. For the present I accept the hypothesis suggested by Kingsley (1910) concerning the relations of the occipital region in vertebrates, where he says: "In the vertebrates there is a continuous addition of new somites at the posterior end of the body as in the arthropods and annelids, implying the existence of the equivalent teloblasts at the posterior end. The assumption of budding zones at other points will explain other features noted. Such a zone in the occipital region will allow us to explain the difference in the number of cranial nerves in the Mammals and the Ichthyopsida and yet allow us to accept the homology of the occipital bone throughout the series. The additional nerves are thus to be regarded not as transferred from the neck, but as new or intercalated structures."

Reasoning on this basis, the first post-vagal nerve of *Amiurus* is a new, intercalated formation, possibly associated with the second somite. What part the first somite plays in the development of the occipital region I have not been able to ascertain, if we assume that the first dorsal muscle segment is that of the first metotic somite. In the larval *Salmo*, Miss Willcox found that there were five segments between the posterior end of the otic capsule and the first neurapophysis. Two of these disappear very early in development and have no trace of nerve connexions. The third has a rudimentary nerve which atrophies early. The next two nerves innervate the next two somites and issue from the cranium between the parachordals and the neurapophysis of the first vertebra. These are later enclosed in bone and leave the exoccipital through the same foramen as the hypoglossus. Fürbringer's formula for this

family is b-c-4, thus having one more element in the occipital region than is found in *Amiurus* and adding another vertebra to the cranium. The myotomes which disappeared in this case were those which took part in the formation of the protometameric neocranium, most traces of which have entirely disappeared in the teleosts (Fürbringer). But here, in the larval condition, there are more somites related to the occipital region than in *Amiurus* and yet the ultimate development is the occipital bones. If we assume with Fürbringer that there are more vertebrae in one case than in the other, our homologies are no longer such, but are analogies of structure without any natural relationship. Even within one family it would be possible to have an exoccipital vertebral articulation which was not constant, allowing for the attachment and detachment of vertebrae. If we assume that the first vertebra, however modified by specialization, remains constant throughout the series, and that the changes in the occipital region are brought about by intercalation of parts, then our homologies and our basis for natural relationship are maintained throughout all the groups.

Jordan (1893) in his work on the relation of the number of vertebrae and the distribution of fishes has shown conclusively that homologies cannot be based upon numerical sequence. He counted the number of vertebrae in closely related species of teleosts from northern and tropical waters and found that the tropical forms usually had the smaller number. The cranial nerves and bones were constant and yet there were cases of intercalation and excalation of the vertebrae.

Schauinsland (1906) has also shown that vertebrae can be intercalated, and that myotomes, nerves and blood vessels of the body cannot be serially homologized. There are various degrees of intercalation, from the presence of both arches, nerves and myotomes, to the absence of one or two of these elements. These facts give conclusive evidence that the nerves leaving the cranium posterior to the vagus cannot be serially homologized with free spinal nerves.

*The Maxillary region.* The premaxillary ossification, one of the few centers of ossification appearing in the cranium at this stage, is a thin horizontal osseous plate lying beneath the anterior end of the ethmoid cornu and extending posteriorly below the nasal organ forming the anlage of the nasal fossa floor (Fig. 18). It is connected with the ethmoid cartilage by a few strands of fibrous connective tissue, and with its fellow of the opposite side, but otherwise lies free in the mass of embryonic connective tissue in this region. Five or six developing teeth are attached to the ventral surface of the ossification.

Schleip (1903) says that the bone and the teeth arise separately in *Salmo* and fuse later. In the youngest *Amiurus* I have studied, the earlier stages have already been passed through, but some tooth germs lie below, unconnected with the posterior part of the ossification, and lend support to the view that *Amiurus* resembles *Salmo* in this respect. The ascending part of the ossifica-

tion in *Salmo* is lacking in *Amiurus*, but that which extends medially beneath the cranium corresponds in the two forms. I find no trace of a labial cartilage in *Amiurus*. In *Salmo* this lies between the cartilage of the ethmoid plate and the premaxillary ossification.

In the 10 mm. *Amiurus* the maxillary bone is represented by a small ossification lateral to the anterior end of the palatine cartilage (Fig. 30). The medial surface of this piece curves half way around the palatine cartilage and a small process projects laterally from its external surface, above the proximal end of the maxillary barbel. There are no teeth connected with the ossification. In *Salmo*, (Schleip, 1903) the maxillary ossification abuts against the palatal cartilage in the same region as in *Amiurus*, but teeth arising below it fuse with it later.

The palatine cartilage is a slender cylindrical bar lying lateral to and parallel with the ethmoid plate (Figs. 1, 2). It is not uniform in diameter, but tapers posteriorly. Its anterior end lies lateral to the nasal organ (Fig. 30) and posterior to it the medial surface is flattened for articulation with the lateral surface of the ectethmoid process. The posterior end of the palatine cartilage is connected with the anterior end of the pterygoid cartilage by a thin stroma of connective tissue cells, among which I was unable to find any cartilage cells. Muscle fibres extend to the dorsal and ventral surfaces of the posterior end of the cartilage from the margin of the ethmoid plate ventral to the orbital foramen.

The pterygoquadrate cartilage consists of an anterior, slender, flat pterygoid bar and a posterior thickened quadrate cartilage (Fig. 1). The pterygoid part extends anteriorly beneath the eye, parallel with the trabecula cranii and connected to it by a sheet of muscle fibres. It ends there and is connected with the posterior end of the palatine cartilage by the stroma of cells, mentioned above. Its posterior end descends obliquely toward the lower jaw and passes into the quadrate cartilage just dorsal to its articulation with Meckel's cartilage. The ventral anterior surface of the thickened quadrate cartilage is concave where it articulates with the dorsal surface of Meckel's cartilage; postero-dorsally the quadrate is indistinguishably fused with the hyomandibular cartilage.

The anterior end of the dorsal margin of the hyomandibular cartilage abuts against the latero-ventral surface of the posterior end of the alisphenoid cartilage (Fig. 1). From this point the articular surface for the hyomandibula extends obliquely dorso-posteriorly along the lateral wall of the otic capsule to a point external to the lateral semicircular canal. From this articulation the hyomandibular descends, as a thin vertical plate of cartilage, from the wall of the otic capsule behind the quadrate and is connected at its ventro-posterior end with hyoid cartilage by the interhyal. Its anterior ventral margin encloses the hyomandibularis branch of the facialis nerve. A cartilaginous process

for the support of the operculum projects from the posterior margin just below its articulation with the otic capsule.

The opercular bones are present at this stage as thin curved sheets of fibrous connective tissue posterior to and below the hyomandibular cartilage.

Meckel's cartilage has fused in front with its fellow of the opposite side forming a continuous lower jaw. The anterior part of the cartilage is slender and cylindrical, but posteriorly, just before articulation with the quadrate, there is a sharp process on the dorsal surface and the dorso-ventral diameter is greatly increased. A small piece of the cartilage extends posteriorly beyond the quadrate articular surface.

In Elasmobranchs (Holocephali excepted) the palatine cartilage is continuous with the pterygo-quadrate bar and abuts against the lateral surface of the trabecula by the palatal process. Its anterior extent is not as great as in *Amiurus* and it never comes in contact with the ectethmoid process, but fuses with the pars palatina of the opposite side forming a complete upper jaw. Since it is supported by the hyomandibula posteriorly and touches the cranium anteriorly, this type of jaw has been termed amphistylic. By dismemberment of the primitive upper jaw of the Elasmobranchs, the condition of *Amiurus* is brought about, and the palatine part of the arch is separated from the pterygoquadrate part. Steps in this process occur in the ganoids (*Polypterus*) and in the teleosts (*Salmo*). In *Polypterus* (Budgett, 1900) the palatine is continuous with the pterygoquadrate part, as in the Elasmobranchs, but has an extent much greater anteriorly. There is no palatal process as in the latter group and the anterior end is attached to the ventral surface of the nasal capsule. In *Salmo* (Parker, 1872; Gaupp, 1906) the palatine cartilage is at first independent and secondarily fuses with the pterygoquadrate. It articulates with the ventral surface of the ectethmoid process, and, at a point anterior to this, with the ventral surface of the solum nasi. The part of the palatine which articulates with the ectethmoid process is club-shaped and larger than the more posterior part. Thus there are important differences in the shape of the cartilage and the manner of articulation when compared with *Amiurus*. The wider separation of the palatine cartilages and their articulation with the lateral surface of the ectethmoid process may be the result of the depression of the cranium. In *Gymnarchus* (Assheton, 1907) the palatine part of the palatopterygoid cartilage is fused with the ventral surface of the cranium, thus differing radically from the condition in *Salmo* and *Amiurus*.

In all of the forms referred to above, with the exception of *Amiurus*, the quadrate is a thickened mass of cartilage connected anteriorly with the pars palatina by the pterygoid cartilage and bearing on its ventral posterior part a surface for the articulation of Meckel's cartilage. The quadrate cartilage of *Amiurus* corresponds in its relations to those of the other forms, but it is fused dorso-posteriorly with the hyomandibula (Fig. 1). In *Polypterus*, the hyomandibular cartilage is dumbbell-shaped, one of its clubbed ends articulating

dorsally with the wall of the otic capsule and the other descending posterior to, but separate from, the quadrate cartilage. Unlike *Amia*, *Amiurus* and *Salmo*, it does not enclose the ramus hyomandibularis facialis. In *Amia* (Van Wijhe, 1882) the palatine and pterygoid cartilages are fused and have an articulation with the ventral surface of the ectethmoid process. In the latter forms the hyomandibular has a greater extent of articulation than in *Polypterus*, but the foramen for the hyomandibularis nerve is nearer the anterior edge of the cartilage in *Amiurus* than it is in *Salmo*. In the latter the quadrate lies much farther anterior to the bulk of the hyomandibula than it does in *Amiurus*, and a slender cartilaginous process descends below it from the anterior end of the hyomandibula. This is the symplectic element which is not independent in *Amiurus*, but is fused with the quadrate-hyomandibular mass of cartilage and may be the part which descends behind the quadrate and connects with the interhyal.

In all of these forms Meckel's cartilage has the same general shape and relations. The articular surface may be convex as in *Amiurus* or concave as in *Acanthias*. Usually a small bit of the posterior end projects beyond the quadrate. The coronoid process on the dorsal surface of the cartilage is well marked in *Polypterus*, but does not project as abruptly as in *Amiurus*. In *Salmo* the cartilage has practically the same size from anterior to posterior ends.

#### THE SKULL OF THE 32 MM. LARVA

The description given in the following section is based upon the study of the head region of 20 mm., 32 mm., and 60 mm. larvae. The first two stages were specimens of *Amiurus nebulosus* (catus), and the third of *A. melas*. A wax model of the cranium of the 32 mm. stage was made, as it gave all of the typical perichondrial and dermal ossifications at an intermediate stage in their development. One side of the model was left without osseous parts, to facilitate comparisons, as is commonly done in modelling of this kind. The 20 and 60 mm. stages were used to supplement this.

Nearly the whole roof of the cranium at this stage is covered by either perichondrial or dermal ossifications (Fig. 3). The former are derived from the ossification of the perichondrium of the chondrocranium and the latter from the ossification of connective tissue membrane external to it. Sometimes the two elements are intimately fused. Another type of bone development may be mentioned here, the ossification around a lateral line canal. The development of this type of bone has been worked out in detail by Platt (1893) and Klaatsch (1895).

The roof is no longer widely open as in the younger stage, but the fontanelles are limited to narrow slits, anteriorly between the frontals and posteriorly between the parietal part of the supraoccipital ossification (Fig. 3). The nasal region has an internasal septum which has grown up from the floor of the ethmoid plate, separating the olfactory lobes (Fig. 22).

In all parts of the cranium the cartilage is more massive and there are very few places where ossification has proceeded far enough to replace it entirely. The fenestra hypophyseos (Fig. 3) is narrower and is closed ventrally by the elongate parasphenoid ossification (Fig. 4). The cranium has grown 6 mm. in length since the 10 mm. stage, and is relatively much flatter. Detailed descriptions of the various cranial regions follow.

*The ethmoid region.* This part of the cranium differs considerably from the younger stage. The olfactory lobes are no longer in the very anterior region of the ethmoid plate, lateral and internal to the olfactory foramina (Fig. 30), but lie farther posteriorly, and a massive internasal septum has grown up between them (Fig. 22). The foramina, instead of lying in an antero-posterior plane parallel to the long axis of the body as in the 10 mm. stage, now lie almost at right angles to it (Fig. 3).

The ethmoid cornua, formerly wide blunt processes separated by a slight indentation, are now narrow and pointed, with a deep notch between them (Fig. 3). The floor of the nasal fossa (Fig. 22), the solum nasi of Gaupp, is wider and thicker than in the 10 mm. stage, although even now it does not extend as far laterally as the palatine cartilage. The ectethmoid process (Figs. 3, 4) described earlier as projecting from the cranial wall at the junction of the ethmoid and alisphenoid cartilages, forms an oblique ridge in the cranial wall above the orbital foramen (Fig. 39) and the anterior part of the orbit. The foramen orbitonasale is more posterior, evidence that the cranial parts anterior to it have elongated. The process in the dorsal part of the cranial wall has grown medially and has fused with the internasal septum to form a rudimentary tegmen cranii (Fig. 3).

The anterior margin of the fenestra hypophyseos, formed by the fusion of the anterior ends of the trabeculae, lies midventral to the optic foramina (Fig. 4), and farther posterior than in the younger stage. The orbital foramen is in approximately the same position as in the younger stage, but the posterior dorsal margin of the ectethmoid process now lies above it (Fig. 39). The foramen is limited by a perichondrial ossification between its ventral and dorsal margins, so that a small aperture is all that remains of the larger foramen of the 10 mm. stage. These ossifications are continuous anteriorly with the perichondrial ossifications on the posterior wall of the ectethmoid process.

A perichondrial ossification on the dorsal margin of the olfactory foramen encloses a branch of the internal carotid artery passing from the cranium to the nasal sac. The olfactory tract, from lobus to the olfactory foramen, is entirely enclosed within the cranium. The development from the condition in the younger stage, has kept the lobus close to the brain, while the anterior end of the cranium grew forward and pulled the olfactory organ with it, resulting in an elongate tractus olfactorius. This stage of the development of the olfactory relations is comparable to that of the Selachian type as has been pointed out in the Cyprinidae by Sagemehl (1891)



The dorsal surface of the roof of the internasal septum is surmounted by a pair of dermal ossifications (Figs. 3, 22) which lie on each side of the median line of the head. Near the anterior end of the cranium they fuse to form a single median plate. The anterior ventral surface of this plate is fused to the underlying perichondrial ossification by osseous trabeculae; posteriorly there is a layer of connective tissue between these two ossifications. The paired posterior pieces of the dermal ossification interdigitate with the anterior ends of the paired frontal ossifications above the posterior end of the internasal septum. The dermal element is the beginning of the dermo-supraethmoid part of the adult bone, and the perichondrial, the auto-supraethmoid part.

In the 60 mm. stage these ossifications have covered the ethmoid cornua and extend laterally above the anterior end of the nasal fossa. There is also a perichondrial and a dermal ossification on the ventral surface of the ethmoid cartilage, which, though not apparent in the 32 mm. stage, are well developed, and fused with each other in the 60 mm. stage. Both dorsal and ventral dermal elements extend anteriorly beyond the cartilaginous cornua and fuse with each other, forming a sharp anterior cranial edge, notched medially. A small pocket is left in the wall of the nasal fossa between the lateral edges of these ossifications which persists in the adult. The rudiment of the premaxillary bone is fused to the ventral surface of the ventral dermal ossification.

A thin flat plate of osseous tissue, derived from the ossification of a membrane, lies along the lateral margin of the dorsal part of the ectethmoid process (Figs. 3, 4). It projects laterally above the anterior end of the orbit and the orbital foramen, and is the dermal portion of the ectethmoid ossification. The rest of the ectethmoid process has hardly begun to show signs of ossification and yet this dermal part extends from the anterior end of the orbit to the palatal articular surface (Fig. 3). Perichondrial ossification has taken place on the ectethmoid process around this articular surface (Fig. 4), but the surface itself remains unossified. Thus the early ectethmoid bone has both auto and dermal parts.

Two lateral line bones, the nasal and the lacrimal (Fig. 3, 22), form a part of the roof of the nasal fossa on each side. The nasal (*na*) is a long straight ossified tube extending parallel to the supraethmoid and separated from it by a narrow space. It contains the anterior end and opening of the supraorbital latero-sensory canal. The process of the formation of such a bone as this has been described by Platt (1893) and Klaatsch (1895), so that it is unnecessary to repeat it here.

The lacrimal lies near the ventro-lateral margin of the roof of the nasal fossa and contains the anterior end of the suborbital latero-sensory canal. Its triangular outline is due to the division of the canal into two tubes for communication with the exterior. Ventro-posteriorly it articulates with the anterior ossicle of the infraorbital series (Fig. 3) and anteriorly it is fastened by connective tissue to the dorsal surface of the palatine ossification (*pal*). Be-

tween the posterior portions of this bone and the more medial nasal, the roof of the nasal fossa is formed by the cartilage which supports the nasal barbel (Fig. 22). This has no connexion with the chondrocranial cartilage and has been named, the 'Nasenflügelknorpel,' in the Characinidae by Sagemehl (1885), who regarded it as the phylogenetic remnant of the nasal-flap cartilage of the Selachians.

The rudiment of the vomer (Figs. 4, 22) appears as an unpaired dermal ossification ventral to the perichondrial ossification on the inferior surface of the ethmoid cartilage. These two ossifications are distinct and have no connexion as did the two types of ossification on the superior surface. There are no teeth on the early vomer, which interdigitates posteriorly with the anterior projections of the parasphenoid ossification by two pointed processes. This interdigitation takes place below the posterior margin of the ethmoid cartilage.

The ethmoidal region of the developing Ganoids is, as far as is known, entirely cartilage at a stage comparable to the 32 mm. stage of *Amiurus*. The only place where perichondrial ossification has appeared is around the ectethmoid process. The supraethmoid ossification is a distinctly dermal bone, comparable to the dermo-supraethmoid of *Amiurus*, but has a transverse lateral-sensory canal ossification on its dorsal surface connecting the supra-orbital canals of the two sides. There is always a space, usually filled with connective tissue, between this ossification in the Ganoids and the underlying cartilage. The nasals of *Amia* are very much larger and flatter than the corresponding bone in *Amiurus* and lie on the ethmoid cartilage. These bones are developed in connexion with the latero-sensory canal system and enclose the anterior ends of the supraorbital canals. The large nasals limit the supraethmoid, so that it remains as a small triangular ossification at the anterior tip of the cranium. The massive internasal septum of the adult *Amia* is comparable to the same element of the 32 mm. *Amiurus*. The prefrontal ossification (my ectethmoid) of *Amia*, is limited, even in the adult, to a small area around the dorso-lateral margin of the ectethmoid process; whether or not it develops perichondrially is not known. The vomer in *Amia* is paired and toothed on its ventral surface, and is limited, as is the vomer of *Amiurus*, to the medial part of the ventral surface of the cranium. As in *Amiurus*, the palatine articular surface remains as cartilage.

The ethmoidal region of the 32 mm. *Amiurus*, in its cartilaginous parts is somewhat like that of a 25 mm. *Salmo*, as described by Gaupp. There is the same massive cartilaginous internasal septum flanked by the nasal fossae, but the anterior end of the ethmoid cartilage is rounded in *Salmo* and no ethmoid cornua are present. The postero-dorsal extent of the ectethmoid process is approximately the same in both cases, relative to the anterior end of the orbit, but the foramen orbito-nasale is much higher in the cranial wall and farther

posterior in *Amiurus* than in *Salmo*. The large tectum cranii is not present in *Amiurus*.

The oblique eye muscles of *Amiurus* have no relation to the ventral surface of the ethmoid cartilage as in *Salmo*. Because of the development of an interorbital septum, the trabecular wall of the orbit has disappeared and the olfactory nerve crosses the orbit and penetrates the ectethmoid process to reach the olfactory organ. Gaupp (1906) probably selected the salmon as his type of teleost development because of the ease of obtaining material, although it is more highly specialized in many parts in which the Siluroids are almost schematic. The ethmoid region is an example of this, and I think the general development of the ethmoidal region in the Siluroids is more primitive than is the same region of *Salmo*.

Gaupp says (06; p. 676): "Die Ersatzknochen occupieren das Chondrocranium bei den Teleostiern in sehr verschiedenem Umfange; meist bleibt ein sehr beträchtlicher Teil von ihm in knorpeligen Zustände erhalten. Die Zahl der einzelnen Ersatzknochen ist dabei ziemlich gross, aber ihre Ausdehnung ist beschränkt. Und zwar können, wie bei den Ganoiden, nicht nur zwischen den einzelnen Stücken grösseren Knorpelzonen bestehen bleiben, sondern bei manchen Formen dringen die Knochen auch nur wenig in die Tiefe des Knorpels ein, so dass die Zerlegung des Knorpelschädels in knocherne Territorien sehr unvollständig sein kann (*Alepocephalus rostratus*, Gegenbaur). Die Ethmoidalgegend bleibt häufig in grössten Ausdehnung knorpelig."

The ectethmoids of *Salmo* (pleurethmoidale, Gaupp) are formed by perichondrial ossifications around the ectethmoid process and a ligamentous connexion with the palatine ossifies with them. A large laterally lying dermal ossification such as is found in *Amiurus* is not mentioned.

When ossification first appears in *Gasterosteus* (Swinerton, 1902), the ethmoid region of the cranium is greatly elongated in a manner somewhat comparable to the condition in *Amiurus*. The preethmoid cornua are very elongate and have a separate ossification not found in *Amiurus*, but which Swinerton compares to the septo-maxillary bones of *Amia*. Concerning the mesethmoid (supraethmoid, author), he says: "In the anterior portions of the skull the expanded plate-like portions of the parethmoid cornua have given rise to the parethmoid bones (figs. 4, 9, *e p b*), whilst a center of ossification, the mesethmoid, has appeared on the dorsal surface of the corresponding cartilage. The edges of the latter ossification extend freely into the surrounding tissue, and give the impression of a membrane bone whose central portion has united with the cartilage leaving the edges quite free."

Evidently Swinerton did not study the histological relations of this dermal plate to the underlying cartilage or he would probably have observed a condition similar to that in *Amiurus* and what Allis (1910) found in the young *Scorpaena*. The latter author says: "The mesethmoid of *Scorpaena*, although undoubtedly a so-called primary bone, consists of two distinctly different portions.

One of these portions is a thin dense layer of superficial bone. The other portion is a deeper one, of quite different appearance, which underlies the central portion only of the superficial portion, and there replaces portions of the cartilage of the skull. . . . The superficial portion of the bone is represented by a thin plate that lies closely upon the cartilage of the skull, without intervening membrane, and must primarily be wholly of perichondrial origin; But this perichondrial plate receives at certain places, accretions or additions to its outer surface, and these accretions, although they present in sections exactly the same appearance as the perichondrial plate, seem to be of purely perichondrial origin. This is particularly noticeable, in my specimens, along the lines of articulation of the mesethmoid with the frontals, and in the mesethmoid process."

This is identical with the condition in *Amiurus*. The ectethmoidal relations are also practically identical in the two forms. They are both of perichondrial origin with a dermal ossification in the form of a large wing of bone added to them. The other relations of the ethmoidal bones are best discussed in connexion with the adult cranium.

*The orbital region.* The orbital wall of the cranium at this stage is formed by the persisting and enlarged alisphenoid cartilage (Figs. 3, 4), together with the ossifications above and below it. It extends from the posterior face of the ectethmoid process as far posteriorly as the anterior end of the otic capsule. The cartilage in this region has grown considerably since the 10 mm. stage, but it has approximately the same topographical relation to the otic capsule and to the optic, trigeminal and facial nerves. The dorsal margins for the foramina of these nerves is as yet formed by the unossified cartilage.

Below the ectethmoid process the cartilage of each wall fuses with the anterior end of the trabecula cranii of that side and, as in the younger stage, forms the posterior margin of the orbital foramen, separating it from the optic foramen (Fig. 4). The posterior margin of the latter foramen has developed from the ossification of the membrane which, in the 10 mm. larva, extended from the alisphenoid cartilage to the trabecula. This ossification (Fig. 32) is not a continuum, but is divided into a dorsal and ventral part. The dorsal part is continuous with the perichondrium of the alisphenoid cartilage as was the membrane of the young animal, but the relations of the ventral part are not so simple and will be taken up in the discussion of the trabecular region. This ossified wall is continued as far posteriorly as the trigeminal nerve (Fig. 4) and forms the anterior margin of its foramen; the dorsal margin has been described above as formed by the alisphenoid cartilage proper (*alis. c.*). The posterior margin of this foramen, through which the main branches of the facial nerve also issue, is formed by a perichondrial ossification (Fig. 4) between the ventral wall of the otic capsule and the posterior end of the trabeculae.

The foramen for the passage of the ophthalmicus superficialis trigemini (Fig. 4, *oph. V.*), which earlier was entirely in cartilage, has now ossified on its ventral external side, so that the nerve is enclosed in an osseous canal posterior to and above the optic foramen. The ophthalmicus superficialis facialis (Fig. 4) issues through a foramen in the cartilage just above the opening of the osseous canal of the ophthalmicus superficialis trigemini and innervates the lateral line canal organs of the anterior part of the supraorbital canal which lie in the frontal and nasal bones (Fig. 11).

The roof of the cranium posterior to the internasal septum is formed by the frontal ossifications (Fig. 3) and the very thin cartilaginous epiphysial bar. The latter is now relatively much farther posterior to the ethmoid region than it was previously and lies in about the same transverse plane as the optic foramina. Dorsally it is covered by the broad frontals, which are separated from each other in the mid-dorsal line by a very narrow fontanelle except in the region immediately above the epiphysial bar where they interdigitate. These frontal ossifications are the largest in the roof of the cranium at this stage; they project laterally above the orbit in continuation with the dermo-oectethmoid (Fig. 4). The ventral surface of the frontal sits on the dorsal surface of the alisphenoid and tegmen cranii cartilages (Figs. 32, 39) and extends down the outside face of the former without being at all intimately connected with the perichondrium of the cartilage. Behind the eye each frontal is grooved for the reception of the suborbital lateral line canal and articulates with the posterior ossicle of the infraorbital series (Fig. 3). The suborbital canal enters the frontal at this point and unites with the posterior end of the supraorbital canal to form a canal which extends posteriorly on to the dorsal surface of the (Fig. 11) sphenotic; this condition persists in the adult. The ossification surrounding the supraorbital canal (Fig. 32.) is indistinguishably fused with the membranous frontal ossification. This canal runs anteriorly within the frontal to a point just posterior to the union of the supraethmoid and frontal, and from here passes into the connective tissue surrounding the posterior end of the nasal bone and thence into the latter (Fig. 11.). From the junction of the supraorbital and suborbital canals, a tubule, enclosed in an osseous canal, runs obliquely posterior toward the middle line of the frontal and opens through a small pore on its dorsal surface (Fig. 3, *t. p.*). Another dermal tubule leaves the frontal through a pore in its dorsal surface just posterior to the entrance of the supraorbital canal into the frontal from the nasal (Fig. 3, *t. p.*)

The infraorbitalia (Fig. 3) are a series of slender, cylindrical, pipe-like bones, beneath and behind the eye, including within them the suborbital lateral line canal. They are six in number, each separated from its successor by the passage of a tubule from the enclosed canal to the external surface of the head, a so-called dermal tubule (Fig. 11.) The most anterior bone of this series connects with the ventro-lateral margin of the lacrimal bone into which the suborbital lateral line canal passes. These bones are typical of the teleosts.

The anterior part of the alisphenoid cartilage, as we have noted, is unossified at this stage (Figs. 3, 4,) and is probably converted into the orbitosphenoid bone of the adult which appears in this region (Figs. 16, 20). The perichondrial ossification between the optic and trigeminal foramina (Fig. 4) is the beginning of part of the alisphenoid bone of the adult (Fig. 20).

In the younger stage the internal carotid artery enters the cranium internal to the trabecula (Fig. 2 ca), but now it has a different relation. This blood vessel enters a rete mirabile, lateral and posterior to the optic foramen, and a branch to the internal part of the cranium enters through the posterior part of the optic foramen. The external carotid enters the cranium as before, between the branches of the trigeminal nerve.

The ramus oticus of the facial nerve (Fig. 3 *rot. VII*) issues through the dorsal posterior margin of the alisphenoid cartilage just anterior to the otic capsule, and proceeds posteriorly within the lateral line canal ossification on the sphenotic bone to innervate a canal sense organ.

Speaking in a general way of the orbitosphenoid development throughout the whole vertebrate series, Parker and Bettany say that it is the result of the ossification of the anterior part of the lateral cranial wall, and may be either anterior to or penetrated by the optic nerve. It also arises from paired centers, although in the adult it may be unpaired. It is described by these authors in *Salmo* as an 'ectosteal' (comparable to my term perichondrial) lamina in the anterior part of each side wall of the cranium. Concerning the development of the same bone in *Salmo*, Gaupp (1906) says that it is developed in the dorso-anterior part of the interorbital septum and the ventral surface of the tegmen cranii of this region, and, further, the olfactory nerve issues through it before entering the orbit. Since an interorbital septum is absent from *Amiurus*, comparison with the *Salmonoid* condition is not very easy and clear to the casual observer. But if we can conceive of the cranium of *Amiurus* being compressed instead of depressed, then the anterior ends of the alisphenoid cartilages, where they unite with the ectethmoid process, would be pushed together, and the surface where they met would be comparable to the interorbital septum. At this stage of *Amiurus* there is no ossification on the dorsal part of the anterior end of the alisphenoid cartilage in the region of the anterior part of the optic foramen, although the perichondrium shows signs of the beginning of a perichondrial ossification, both on the outer and inner surfaces, which extends down to the trabecula. The first traces of the orbitosphenoid occurs in the *Salmon* at the 35 mm. stage.

The alisphenoid of the *salmon* is a later ossification than the orbitosphenoid, whereas in *Amiurus* it is quite well developed before any great development of the orbitosphenoid. Speaking of the alisphenoid in *Salmo*, Gaupp (1906) says: "Entsteht sehr spät (*Salmo fario* von 40 mm.) in Form von zwei perichondralen Knochenlamellen, einer inneren und einer äusseren, auf der knorpeligen Schädelseitenwand vor der Ohrkapsul. Im Anschluss an den

perichondrale entstanden Abschnitt ossifiziert auch ein Teil der häutig gebliebenen Bettenwand der Orbitotemporal region. Das Alisphenoid schliesst in selbständige Foramina den N. Trochlearis und den ersten Ast des Trigemini ein und begrenzt von oben her das Opticum."

The posterior alisphenoid ossification between the optic and trigeminal nerves of *Amiurus* has most of these characters given by Gaupp for the alisphenoid of *Salmo*, who says little about the nature of the 'hautig' wall and its relation to the trabecula. As I interpret it, this wall is developed at a very early age from the perichondrium of the alisphenoid cartilage, since they are intimately connected in the 10 mm. stage. The relations of the ventral part of this region will be taken up later in the discussion of the trabecular region. In *Salmo*, the ophthalmicus superficialis trigemini has a different course through the alisphenoid cartilage and is closer to the otic capsule than it is in *Amiurus*. Gaupp does not discuss the relations of the ophthalmicus superficialis facialis of *Salmo*.

Both alisphenoid and orbitosphenoid ossifications occur very late in the development of the ganoids in approximately the same place in regard to the passage of nerves as in the teleosts. In the Amphibia the orbitosphenoid (sphenethmoid; Parker, 1872) is developed on the anterior end of the alisphenoid-trabecular cartilage and the posterior margin of the ethmoid cartilage, in approximately the same position that it has in *Amiurus*. The alisphenoid ossification does not form.

As mentioned above, Gaupp (1902) claims that the alisphenoid of the mammalian cranium is developed from a newly added cartilaginous part, the 'ala temporalis,' but I have adopted a different view, and believe that the cartilage is the same in both Mammals and Ichthyopsida, because of its relation to the trigeminal nerve. Gaupp himself admits that nerves are good landmarks in the establishment of homologies and yet denies this homology.

The frontal bones first appear developmentally in the Acipenseridae (Parker; 1882) and the lower Siluridae (Hertwig; 1876), as dermal plates, slightly separated from the corium and having their origin in this layer. They never form a pair of distinct frontalia as in *Polypterus*, *Amia* and *Lepidosteus*, but remain as groups of plates. They do not touch the cartilage of the tegmen cranii, but are separated from it by connective tissue. Walther (1882) found that the frontalia in *Esox* develop in the same way, but were nearer the cartilage and had less relation to the corium. Williamson (1851), Heincke (1867), Hertwig (1876), came to the conclusion that the frontals of the teleosts and ganoids were descended from dermal scales, a view now universally accepted for all osseous vertebrates.

Vrolik (1873), in his discussion of the development of the frontals in the teleosts, remarked that they were formed for the protection of the lateral line canal which, in the adult of most teleosts, runs along the dorsal surface of the bone. Walther (1882) in his work on *Esox* denies that such a condition exists,

because the centres of the frontals appear before there is any trace of the lateral osseous canals, and that, in some forms, the osseous canals are entirely separate from the frontals throughout life, but in the majority of forms they fuse with the underlying independent frontal. The frontals of *Amiurus* bear out this latter statement, since the rudiments appear as paired membranous sheets roofing the large fontanelles. The lateral line canal ossification arises independently of this membrane and only secondarily becomes connected with it. This independence of ossifications shows especially well in the relation of the ossification surrounding that canal extending from the junction of the suborbital and supraorbital canals toward the middle line of the head; here the canal ossification is very distinct from the underlying frontal. At this stage in *Amiurus* the frontals have practically the same relations to the surrounding bones that they have in the adult cranium.

The infraorbital chain of bones, whenever developed, is related to the suborbital lateral line canal, and in most cases the component bones of the chain are larger and flatter than in *Amiurus*, a condition usually correlated with the development of the eye.

The anterior ends of the trabeculae are as yet continuous with the posterior end of the ethmoid plate, although the fenestra hypophyseos is more posterior than it was in the younger stage (Fig. 3). They are no longer continuous bars from the ethmoid plate to the parachordal plate, but half way between these regions a part of each has been resorbed and parasphenoid and suprasphenoid ossifications have replaced it by growth dorsally into this region, forming the posterior margin of the optic foramen and part of the margin of the trigeminofacial foramen (Fig. 4).

The trabeculae of the two sides are connected across the anterior end of the fenestra hypophyseos by a perichondrial ossification, separated by a wide space from the more ventrally situated parasphenoid ossification (Fig. 4). This ossification lies in the floor of the cranium between the optic foramina. Anterior to these foramina the trabeculae are united to the anterior ends of the alisphenoid cartilages to form the cranial wall between the orbital and optic foramina as in the 10 mm. stage. Toward the posterior end of the optic foramina, the perichondrial connexion between the trabeculae disappears, and osseous trabeculae, the centre of the suprasphenoid bone, extend dorsally from the parasphenoid ossification, which now forms the medial cavum floor (Fig. 32). Farther posteriorly, the suprasphenoid ossification extends above the trabeculae and meets the lateral margins of the parasphenoid external to them, thus encasing the cartilage in an osseous sheath, unconnected with the perichondrium. In this immediate region, just back of the preceding part, between the optic and trigeminal nerves, the cartilage of the trabecula disappears (Fig. 3), and the suprasphenoid ossification is connected with the parasphenoid by osseous trabecula across the space formerly occupied by the cartilage. The ossification extends dorsally in the cranial wall and, with a ventral ossified spur



from the alisphenoid cartilage (Fig. 4), forms the wall between the optic and trigeminal nerves.

Ventral to the trigeminal nerve, the cartilage reappears within the ossification, but unconnected with it as before. This cartilage becomes larger posteriorly, until, posterior to the passage of the facialis nerve, ossification has again become limited to the median ventral surface and has only a couple of splints protruding into the cavum cranii (Fig. 3) through the anterior fenestra basicranii.

The question now arises as to the proper designation for this part of the basal fenestra, which lies behind the hypophysis, in the salmon (Parker, 1872; Gaupp, 1906) it is termed the fenestra basicranii anterius, in contradistinction to a more posterior parachordal fenestra. The cartilaginous plates on either side of the cranial floor in this region of *Amiurus* have grown anteriorly in concert with the otic capsules, since their lateral ends are confluent with the perichondrial ossification of the ventral side of the otic capsules (Fig. 4). The small medial space between them is a fenestra between the anterior parachordals and is therefore comparable to the corresponding fenestra in *Salmo* and may be so designated. It is evident therefore, that the connexion between trabeculae and parachordals has disappeared by resorption of cartilage. The dorsal ossification on the parasphenoid, the suprasphenoid, has taken its place.

In *Gasterosteus* (Swinerton, 1902) the trabecular cartilage has disappeared in this region as in *Amiurus*, but the floor of the cranium is formed by the parasphenoid, except in the region of the eye-muscle canal; here there is an ossification corresponding to the suprasphenoid of *Amiurus*. Unfortunately the details of the development of this region is not known. The modifications of the basal part of the cranium, in forms having an interorbital septum, where the parts are all compressed, are not easily homologized with the depressed condition of the same region in *Amiurus*, and in making comparisons, this fact always has to be borne in mind. Also the absence of an eye-muscle canal in *Amiurus* makes for differences in the development of the basal parts between the orbits.

In *Salmo* there is an elongate trabecula communis (Parker, 1873; Winslow, 1897; Gaupp, 1906) which is concave below and bears the membranous interorbital septum on its crested dorsal surface. I have found no mention of a perichondrial ossification around this trabecula communis, such as is found at the anterior ends of the trabeculae in *Amiurus* between the orbits, and which is the anlage of the orbitosphenoid of the adult. The parasphenoid has the typical relation to the floor of the cranium that it usually has in the *Ichthyopsida*.

McMurrich (1884b) has described a basisphenoid in this region of the adult *Amiurus*, as an "indistinct ossification completely fused with the parasphenoid." I have remarked above that there is an ossification on the dorsal surface of the parasphenoid between the trabeculae and have it named the supra-

sphenoid. In the piscine nomenclature commonly used at the present time, this ossification is regarded as the basisphenoid, although it has been known for a long time that it is not the homologue of the basisphenoid center of ossification of man, from which the terminology is derived. In all fishes where it appears as a distinct bone, it lies anterior to the hypophysis and is developed from connective tissue membrane. Cuvier called it the 'sphenoide anterieur,' but Hallmann (1837) pointed out that Cuvier's diagnosis of this bone as the homologue of the presphenoid region of man was incorrect. Concerning this bone, Hallmann says: "Ein vorderer Keilbeinkörper wäre wie bei die Säugethieren und wie als der Name sagt, vor dem hintern zu suchen. Aber mit Cuvier (der die Knochen Fig. 24 g und Fig. 25 u. 26 beide vordern Keilbeinkörper nennt) einen auf den vordern Theil des Keilbeins oder auf die Mitte desselben sich herabsenkenden Knochen Keilbeinkörper nennen, heisse aller Analogie."

Reasoning upon this basis and continuing to regard the parasphenoid as the homologue of the basisphenoid of the mammalian cranium, he named the bone in question, the 'sphenoide superior' and maintained that it was found only in fishes and that it had varying developments in these.

Huxley (1864) studied the development of the parasphenoid in *Esox* and concluded that it was a dermal derivative and hence not the homologue of the basisphenoid ossification center of man, a purely cartilage development posterior to and below the hypophysis. He named Hallmann's 'sphenoide superior,' the basisphenoid, but remarked that it was only comparable to the anterior part of the basisphenoid and that the rest of the element persisted as cartilage. His reasons for regarding this bone as the homologue of the basisphenoid are, that in the foetal human skull the basisphenoid contributes nothing toward the posterior boundary of the pituitary fossa, which is formed by the long cartilaginous synchondrosis which connects the rudimentary basisphenoid with the basioccipital. Thus he regarded the bone as a rudimentary basisphenoid. Owen, following St. Hilaire, called it the entosphenal, and regarded the parasphenoid as divided into a presphenoid and basisphenoid part, regardless of the work of Huxley. Allis (1897) regarded it as the homologue of the presphenoid bone of man and yet called it the basisphenoid.

The development of this bone is the keystone in making the homologies, and all who have studied its development have found that it develops from connective tissue membrane anterior to the hypophysis, and hence cannot be the homologue of the basisphenoid bone of man—a cartilage bone developed from the basis cranii. The cartilage which is enclosed within the parasphenoid and this ossification in *Amiurus* may be the homologue of the basisphenoid which never ossifies. This is an ossification peculiar to fishes and, together with the parasphenoid, it becomes gradually replaced in the higher vertebrates by the ossification of the basis cranii. Since it is neither the homologue of the basisphenoid nor of the presphenoid, it must be regarded as a distinct bone and

hence the name proposed a priori by Hallmann (1837), the 'suprasphenoid,' may be applied to it, although it is to be understood that his criteria for distinguishing it are not used as the basis of the terminology, but rather its independence as a connective tissue ossification above the parasphenoid and between the ventral ends of the alisphenoids.

Schleip (1903) says that in *Salmo* the bone arises from a direct ossification of the membranous wall at the anterior end of the eye-muscle canal, and that it is indirectly connected to the parasphenoid and the alisphenoids by membrane which later ossifies. He recognizes it as part of the elements of the primordial cranium which has no cartilage stage and says, p. 378;

"Das Bindegewebe, aus dessen Ossifikation sie hervorgehen, geht in Teile des Knorpelschädels über, verschliesst also lücken, die der Knorpelschädel aufweist, und ist daher wohl nicht zu weit gegangen, wenn man es als Anlage des Primordiacranium gehörig auffasst, als ein Teil desselben, der nicht zur Verknorpelung kommt."

Even assuming this view to be true, the morphological relations of the bone must be considered before it can be called the basi- or presphenoid.

The parasphenoid of *Amiurus* in its development is like the large parasphenoid of the *Urodeles* which develops between the trabeculae and forms the floor of the cranium in this group. Its lateral edges form the ventral margin of the lateral wall of the orbital region as in *Amiurus*. It is related to the orbitosphenoid in the anterior region, just as the parasphenoid of *Amiurus* is related to the ossification around the anterior ends of the trabeculae. In the 10 mm. stage of *Amiurus*, the place occupied by the parasphenoid of the 32 mm. stage is closed by a membrane which is separated from the trabeculae and already shows signs of extending above and below them. In *Amia*, the median floor of the cranium is continuous cartilage, a condition arising from growth medially of the trabeculae, and the whole hypophysial fenestra is closed, except for a small part just below the hypophysis, which is closed by the parasphenoid. The parasphenoid here has the same superficial extent on the ventral surface that it has in *Amiurus*, but its growth dorsally is restricted by the cartilaginous cranial base. The orbitosphenoids of *Amia*, one on either side of the cranium, are situated around the anterior margin of the optic foramina, but do not have the same ventral extent as the ossification around the anterior ends of the trabeculae of *Amiurus*.

*The parachordals.* In the 10 mm. larva of *Amiurus*, the parachordal plates posterior to the hypophysis, were rather widely separated from each other (Fig. 2). Laterally they were continuous with the cartilage of the anterior end of the otic capsules, this cartilaginous connexion forming the posterior margin of the trigemino-facial foramen, (Fig. 2). In the 32 mm. larva this is replaced by a thin lamella of perichondrial bone (Fig. 4). It appears as if this condition arose from the earlier one by a growth of the otic capsule and the

parachordal away from each other, without a corresponding growth of the immediate connecting region.

Posterior to the hypophysis, the parachordals gradually approach each other and the fenestra between them narrows to a mere slit as compared with the wide fenestra in this region of the younger cranium. The parasphenoid ossification forms the floor of this fenestra and a couple of processes from its dorsal surface project into the cavum cranii (Fig. 4, *Ps.*). With fusion of the parachordals with each other farther back, the parasphenoid is excluded from the floor of the cavum cranii and lies ventral to the cartilage thus formed (Fig. 27). In the layer of osteoblasts between the periosteum of the parasphenoid and the cartilage the anterior projection of the perichondrial ossification on the ventral surface of the posterior part of the basal plate, appears as a couple of spicules.

At the line where the parachordals (Fig. 4) fuse with each other, they also form a cartilaginous continuum with the otic capsules, the perichondrium of which is ossified. Laterally and above the parachordal-otic capsule fusion, the cartilage of the capsular wall, which was thick in the younger stage, is reduced to an osseous plate continuous with the perichondrium of the cartilage above and below it (Fig. 4). The edges of this thin region are abrupt and the macula utriculi abut against the wall, giving evidence that the thinness of the wall was caused by the lateral growth of the utriculus.

There is a small recess in the floor of the cranium on either side in the region where otic capsule and parachordal fuse. Each recess is covered dorsally with a thin lamella of bone and osseous trabeculae (Fig. 27) extend across its lumen. Proceeding posteriorly, these recesses converge and the anterior ends of the sacculi appear within them (Fig. 27). These recesses were not present in the younger stage, but have been caused by the anterior growth of the sacculi beyond the canal sinus imparis, and subsequent growth of the cartilage of the floor around them. The osseous roof above these recesses is apparently formed by the ossification of perichondrial strands from this cartilage (Fig. 27). These recesses contain the anterior ends of the sacculi ('processes of Comparetti,' Wright, 1884) and are said to lie within the prootic bones of the adult. For a short distance posteriorly the 'processes of Comparetti' are separated from each other by a median crest of cartilage (Fig. 28), the dorsal surface of which is grooved and filled with osseous trabeculae of perichondrial origin. The sacculi grow larger as they approach the canal sinus imparis (Fig. 28), the median cartilage diminishes in amount and the two recesses come closer together. The osseous roof of each recessus disappears in this region where the ramus saccularis of the auditory nerve descends to innervate the macula sacculi (Fig. 28). Just posterior to this innervation the sacculi of the two sides are connected with each other by the canal sinus imparis.

In the other teleosts whose developmental history has been followed, the ossifications which arise in this region around the anterior parachordals and

the ventral ends of the otic capsules, have been described as the centres of the prootics. Schleip (1903) says: "Die ersten Spuren von Verknöcherung treten bei einem Lachs von 24 mm. Länge auf: das Prooticum besteht hier aus einer inneren und einer äusseren, den Knorpel in der Umgebung des Facialisloches einfassenden perichondrialen Knochenlamelle; ein Zusammenhang beider an der Rändern des Foramen ist aber nirgends vorhanden, vielmehr entbehrt die Wand des Facialiskanals selbst den Knochenüberzug noch vollständig (Siehe Fig. 5). Die genannten Lamellen sind wie überhaupt alle perichondralen Verknöcherungen auf diesem Entwicklungstadium homogen, scharf vom Knorpel wie vom Bindegewebe abgesetzt und haben kein anderes Reliefe, als es durch die Anlagerung an die Knorpeloberfläche bedingt ist; wenige schmal, spindelige Zellen bilden das Periost."

In the salmon, however, the eye-muscle canal is formed by the inward growth of the rectus eye muscles between the parachordalia and the cavum cranii, a membranous bridge roofing the canal so formed, and supporting the brain. The homology between *Amiurus* and *Salmo* in this region is easily seen, despite the specialization in the latter. In both, the parachordalia are continuous with the otic capsules posterior to the hypophysis and there is the narrow fenestra basicranii anterior between them, the floor of which is formed by the parasphenoid ossification. There are the same inner and outer perichondrial lamellae as described by Schleip (1903), but in *Amiurus* at this stage these lamellae have united. The 'processes of Comparetti' do not occur in *Salmo*, but are limited to the *Ostariophysi*. The relations of these processes to the cartilage of the floor of the cavum and to the cavum itself are very similar to the eye muscle relations and have arisen by an invasion of the cranial floor. The thin osseous wall of the otic capsule, described above, is formed in the same way as in *Salmo* (Schleip), by the disappearance of the inner lamella and resorption of the underlying cartilage, so that the wall is formed by the outer lamella alone.

In *Amiurus*, the cartilaginous wall (Fig. 4) lateral to the utriculo-saccular connexion is very thick and is continuous dorsally with the septum semicircularis laterale. That part of the parachordal which contains the sacculus forms an angle of about 120 degrees with the otic capsule proper. The glossopharyngeal nerve issues from the cranium dorso-lateral to the sacculus and between it and the utriculus (Fig. 4). The anterior margin of its foramen is formed entirely of cartilage, (Fig. 4). Posterior to the passage of this nerve the sacculi are again enclosed in recesses as were their anterior ends. The ossifications which form the roof extends transversely from between the two jugular foramina (Fig. 26) and meet by suture medially below the brain. From the ventral surface of each of these ossifications, an ossified bar extends obliquely toward the midventral surface of the basal plate. This basal plate is triangular in cross-section and forms a cartilaginous crest between the recessus sacculorum. It is surmounted by a perichondrial ossification which has two diverging proc-

esses connected by sutures to the descending processes of the roof plates of the recessus sacculorum. Thus there are formed three chambers; the two lateral contain the sacculi and the lagenae, while the medial unpaired chamber contains the sinus impar of the Weberian apparatus, and is called the cavum sinus imparis. The floor of each recessus sacculi is formed by a thin osseous lamella, as the cartilage which was originally in this region has been resorbed and the perichondrial ossification alone remains. The ventral surface of the median basal plate is covered by a thick perichondrial ossification which extends laterally beneath the recessus sacculorum and with which the parasphenoid ossification interdigitates. In cross-section, the notochord appears as a very small circular area within the median basal plate, the tip lying just beneath the region of the canal sinus imparis. In the younger stage it extended anterior to this connexion and in this immediate region was very large in comparison with the amount of the surrounding cartilage. The plate at that stage (10 mm.) was divided into halves (Fig. 8), but now forms a continuum above and below the notochordal tip (Fig. 27).

The amount of cartilage around the notochord gradually diminishes toward the posterior end of the cranium, while the diameter of the notochord increases (Fig. 26). The whole floor of this region has become deeper and narrower than it is anteriorly and the ossification in the floor of the recessus sacculorum has replaced the cartilage entirely. The former cartilage between the glossopharyngeal and vagus nerves, has been resorbed and the lamella formed by the ossification of its outer perichondrium alone is left, separating the two nerves (Fig. 4). The vagus nerve issues posterior to this lamella through a very elongate foramen (*x*) between the otic capsule and the dorso-lateral edge of the recessus sacculi of that side. Posterior to this foramen the perichondrial ossification at the ventral end of the occipital arch is continuous with that on the roof and side walls of the recessus sacculi. This lamella is, however, only an anterior projection of the perichondrial lamella around the anterior surface of that part of the occipital arch which joins the cartilage of the roof of the recessus more posteriorly (Fig. 23). This cartilage is not very great in extent (Fig. 23) and osseous trabeculae again appear between the saccular recesses and the posterior ventral end of the occipital arch. The hypoglossus nerve, which in the younger stage issued from the cranium through a rather large space, is now enclosed within this osseous mass (*ex*).

Solid cartilaginous masses on each side of the notochord mark the posterior ends of the recessus sacculorum, just posterior to the passage of the hypoglossus (*pch*). These cartilaginous masses extend farther posterior than in the younger stage and rise higher on the sides of the notochord (compare Figs. 17, 23) so that there is a groove between them filled with osseous tissue (Fig. 37). The whole notochord is surrounded with osseous tissue and there is an hypochordal cartilage present on its ventral medial surface. This piece of cartilage was not developed in the 10 mm. stage. Anterior to the hypochordal cartilage

the centre of the basioccipital on the ventral surface of the parachordal plate is thick and spongy, and continuous with the ossification surrounding the notochord. The transcapular processes of the shoulder girdle are fused with the perichondrial ossifications on the lateral surface of the posterior end of the parachordals.

McMurrich (1884b), from a study of young *Amiurus*, 20 to 38 mm. long, concluded that there never was a preformation of cartilage in the floor of the sacculi in this region. Cartilage occurred here in the 38 mm. stage, but he stated that it was due to the growth anteriorly of the cartilage at the very posterior end of the cranium. I have observed cartilage in this region in the 10 mm. stage, and the ossification at the 32 mm. stage which forms the floor of the recessus sacculorum is the result of the perichondrial ossification of the original cartilage, the cartilage itself having been resorbed.

The anterior processes of the scaphia, which, in the 10 mm. larva, lie immediately dorso-lateral to the notochord (Fig. 12), are now separated from it by paired cartilaginous masses (Fig. 37), the posterior continuation of the posterior parachordalia. These are covered ventrally with the perichondrial anlage of the basioccipital and latero-dorsally with that of the exoccipital. Posterior to this region the notochord is relatively much larger than it is intercranially. The endorhachis which supports the spinal cord and divides the sinus impar into the atria sinus imparis is more compressed than in the younger stage. It widens posteriorly in the region where the anterior processes of the scaphia fuse with the scaphia proper (Fig. 29), which are as yet of cartilage and articulate by rounded surfaces with the notochord. The claustra are better defined than in the younger stage; they lie between the scaphia and the anterior end of the third neural arch, forming the wall of the vertebral canal in this region. The second post-vagal nerve issues posterior to the scaphium (Fig. 35). The most striking morphological feature of this region is the posterior growth of the parachordalia and the subsequent separation of the anterior processes of the scaphia from the notochord (Fig. 37). The enclosure of the hypoglossus nerve within the cranium by ossification (Fig. 23) is comparable with the history of the same nerve in *Gasterosteus* (Swinerton, 1902) and the first two post-vagal nerves of *Salmo* (Harrison 1895; Willcox, 1899).

Schleip (1903) has described the formation of the ossifications around the parachordal cartilages and the ventral parts of the otic capsules in *Salmo*. He describes the basioccipital ossification as arising from paired inner and outer lamellae on the parachordals in the region of the fenestra basicranii posterius, into which the notochord projects. Anterior to the notochord the inner and outer lamellae meet across this fenestra, but in the region of the notochordal tip they are separated from each other by an osseous mass around the notochordal sheath, which he calls the 'ausfüllende Knochenmasse.' In *Amiurus* there is no fenestra around the anterior tip of the notochord and the ossification on

the inner perichondrium forms the walls of the *cavum sinus imparis*. The outer lamella is unpaired and is thicker in the middle line than on the sides, a contrast to the paired outer lamellae of *Salmo*. The paired *rectus externus* muscles are located in this region in *Salmo*. Further posterior in *Salmo*, the outer lamella has a spongy appearance, comparable to the appearance of the osseous lamella in the same region of *Amiurus* and which Schleip says arises from the ossification of fibrous connective tissue in that immediate region in connexion with the perichondrial ossification of the basal plate. From this comparison, I have concluded that the ossifications in this region are homologous and that they are the centres of the basioccipital of *Amiurus* as they are of *Salmo*.

The osseous lamella around the glossopharyngeal and vagus foramina and the ventral ends of the posterior semicircular canal and above the *recessus sacculorum* and *cavum sinus imparis*, have been described by Schleip and Gaupp as the centres of the exoccipitals. In *Amiurus*, the part above the *sinus impar* is preformed in membrane and only secondarily connects with the perichondrial ossification and hence cannot be exoccipital, though fused with it. The hypoglossus, in both *Salmo* and *Amiurus*, was not included within the cranium at an earlier stage, but is now enveloped in an osseous sheath between parachordal plate and the occipital arch.

*The otic capsules.* The cartilage enclosing each membranous labyrinth has grown considerably since the 10 mm. stage, but the relations of the septa semicirculares (Fig. 7) have remained the same. The detailed description of these, given for the younger stage, will also fit the 32 mm. stage and the adult, except for a change in size. The parts which merit description at this 32 mm. stage are the centres of the otic bones, which, in the teleosts, include prootic, sphenotic, pterotic, epiotic, and opisthotic. All except the last are present in *Amiurus*, according to McMurrich (1884b), and the problem is to locate and describe them in their earliest form.

These bones were first grouped as the otica by Huxley (1864), who called attention to the fact that they were developed around the otic capsule, which, as cartilage, had an independent origin and only secondarily became connected with the parachordalia and the occipital arch. Hence these bones formed a natural group in comparison to the other bones of the cranium. Vrolik (1873) objected to grouping of these bones as otics, and, because of the relation of the occipital bones to the labyrinth, maintained that these also could be included with the otica. As Van Wijhe (1882) later pointed out, this was due to a misunderstanding of the original statement of Huxley, because it is a well-known fact that the membranous labyrinth invades other bones than those which are developed around the capsule. Vrolik also claimed that the otic bones took no part in the formation of the cranial wall because he found the opisthotic to be variable bone, sometimes developed in the cartilage of the capsule wall,



again not related to the cartilage, and sometimes entirely wanting. We have no reason to believe that at some stage in the phylogenetic history of the vertebrates there was another ossification forming the wall of the cranium in place of the otic capsules of today. Could we prove that the otic capsule superseded an osseous or cartilaginous brain-case wall, only then could we say that the otic bones were not parts of the brain case.

The sphenotic is the most anterior dorsal of the otic bones and according to those who have studied its development in the teleosts, it appears as an ossification around the dorsal anterior end of the cartilage of the anterior semicircular canal recess, and of a part of the posterior end of the alisphenoid cartilage. In the 30 mm. *Salmo* (Schleip, 1903), the first sign of this ossification is an osseous lamella in the perichondrium of the postorbital process, which forms a ledge of bone projecting laterally above the hyomandibular articular surface and extending posteriorly along the roof of the anterior semicircular canal. The levator operculi muscle is attached to its outer surface. It spreads dorsally on the surface of the cartilage as far posteriorly as the pterotic ossification (which is developed on the roof of the lateral semicircular canal) and ventrally as far as the hyomandibula. At a later stage another perichondrial lamella is formed on the inner surface of the roof of the anterior semicircular canal. The formation of the adult bone takes place by the resorption of the cartilage between these two layers and by endochondrial ossification. Schleip makes no mention of the development of a lateral line canal ossification in connexion with the outer lamella. A fine nerve issues through the cartilage and bone in this region to innervate the sense organ of the lateral line canal contained in the pterotic ossification.

In the development of the sphenotic of *Gasterosteus* (Swinerton; 1902), the inner lamella and the cartilage disappear, so that the wall is formed by the outer lamella alone.

In the 32 mm. larva of *Amiurus*, ossification is advanced, but I did not find any ossifications in this region of the 20 mm. larva. The ossification enclosing the supraorbital lateral line canal is intimately connected with the perichondrial ossification on the outer surface of the cartilage forming the roof of the recess for the anterior semicircular canal (Fig. 19). Just anterior to the cavum of the anterior semicircular canal, the ramus oticus of the facial nerve (the fine nerve of *Salmo*, Schleip, 1903) issues through the cartilage (Fig. 3) and divides into anterior and posterior branches; the posterior continues within the lateral osseous canal to innervate the next sense organ of the canal system. The perichondrial ossification and that of the lateral line canal cannot be distinguished from each other. Although there was no ossification in the 20 mm. stage in this region, the beginning of the lateral line ossification was represented by a heavy tract of osteoblasts surrounding the membranous canal. With subsequent ossification, the bone thus formed fused immediately with the underlying perichondrial ossification of the alisphenoid cartilage and the otic capsule. The

cavum of the anterior dorsal end of the skeletal anterior semicircular canal is filled with osseous trabeculae extending between the osseous lamellae in the perichondrium of its walls (Fig. 36). The outer lamella extends down on the side wall of the capsule as far as the hyomandibular articulation, but does not enter into the formation of the articular surface, which is as yet of cartilage. The abductor hyomandibularis muscle and the levator operculi are attached to the outer lamella, the former having the broader surface of attachment.

A part of the cartilage in the roof of the anterior semicircular canal recess has been resorbed together with the outer perichondrial lamella, so that the inner lamella forms the wall between the cavum of the recess and the lumen of the lateral line osseous canal (Fig. 19). This is just the reverse of the process that Schleip observed in *Salmo*, where the inner perichondrial lamella disappeared first. Toward the posterior end of the hyomandibular articular surface, the outer perichondrial lamella disappears and the lateral line ossification alone remains; it is separated from the underlying cartilage by fibrous connective tissue. This is the posterior end of the sphenotic, and when the perichondrial lamella appears again, it is on the dorsal surface of the lateral semicircular canal region of the otic capsule and is the centre of the pterotic ossification.

In the 60 mm. stage, cartilage resorption in the roof of the anterior semicircular canal recess has gone still farther, the outer and inner lamellae are indistinguishably fused with each other (Fig. 33), and endochondrial ossification has occurred, so that the place originally occupied by cartilage is now filled with osseous trabeculae. The cartilage near the posterior end of the roof of the recess still persists, and a thicker and spongier osseous mass projects laterally above the hyomandibular facet. Behind this, as in the 32 mm. stage, the lateral line ossification of the surface of the sphenotic passes on to the surface of the squamosal part of the succeeding ossification.

The ossification surrounding the lateral wall of the recess for the lateral semicircular canal, is the squamosal of most authors and the pterotic of Parker (1873). As part of the bone is preformed in cartilage and part of it of membranous origin a combination of these two names is preferable as it implies relationships which neither term used alone would signify. Hence I propose the name squamoso-pterotic for this mixed ossification.

Allis (1899) made a detailed study of the descriptions of this bone in different groups of fishes by the investigators before him. He says, in summarizing his review: "We thus see that the squamosal of fishes is composed of a canal component and a deeper lying component which may be either a so-called membrane bone, or such a bone fused with a so-called primary ossification. The primary ossification may be wholly wanting, and perhaps the canal component also. Furthermore the canal component may be found entirely separated from the underlying bone, may be found fused simply with an underlying membrane component, or may be fused with such a component and with a so-called primary ossification, which latter ossification alone is traversed by the

semicircular canal. The canal component, apparently always united with the underlying membrane bone, may as a so-called dermal bone, be found fused with other, adjoining dermal bones; while the primary ossifications may be fused with other adjoining primary ossifications (*Ctenodus*), or with such ossifications and the intercalar (*Polypterus*). It is the primary part of the bone, and not its 'Deckenknochenanteil' that gives articulation to the hyomandibular."

Throughout the discussion he does not give any reason for calling this bone the squamosal. The term squamosal signifies a homology with the squamosal of the Tetrapoda, which only a part of this compound bone of the fishes has. According to the researches of Thyng (1905) on the squamosal bone of the Tetrapoda, some of the criteria for the establishment of its identity throughout the series were as follows: "The term squamosal, including its various forms, was first applied to an element in the human skull which later fuses with others to form the temporal bone. Hence in applying the term to the lower groups the laws of nomenclature demand that it be given to that element which is the homologue of the squamosal in man. It is also evident that all possible criteria should be utilized in settling these homologies, not alone those of adult relationships and articulations, but those of development as well. . . .

"The development of the mammalian squamosal shows it to be a membrane bone which overlies the otic capsule and is at first intimately connected with the incus (quadrate) by a dense and fibrous stroma. Hence it must be concluded that close association with the quadrate (incus) and the otic capsule is the primitive relation of the squamosal, and therefore, the most important criterion in ascertaining its homology in the non-mammalian vertebrates."

Comparing the above with the statements of Allis, it is clear that the only bone in the fishes which may be compared to the mammalian squamosal is that dermal ossification which overlies the otic capsule above the lateral semicircular canal. The question of connexion with the underlying primary ossification is secondary, as is also that of the quadrate, for in the fishes the quadrate is separated from the cranium by the hyomandibular. The true squamosal would therefore, be the dermal ossification, described by Allis as lying above the cartilage of the wall of the lateral semicircular canal; it has nothing to do with the articulation of the hyomandibular and is, in the fishes, connected with the lateral line osseous canal. The primary ossification underlying it is the pterotic ossification of Parker (1873) and is just as much a center of ossification of the otic capsule as are the other periotic ossification centers of the mammalian petrosal portion of the temporal bone, although no center has been found corresponding in position to the pterotic center of the otic capsule of the fishes.

Schleip (1903) gives a detailed description of the ossifications in the region of the lateral semicircular canal wall in *Salmo* and follows Gaupp in his nomenclature, naming parts derived from membrane and the lateral line ossification,

the dermosquamosal parts, and those derived from perichondrial ossification the autosquamosal parts. His figures are clear and easy to understand. The outer perichondrial lamella (for there are two, one on the outer perichondrium of the wall and one on the inner) is strongest where it is unprotected by the dermosquamosal. In the younger stages the dermosquamosal was separate from the autosquamosal, but gradually the parts become intimately fused. He cannot say which of the two ossifications appeared first. Toward the posterior end of the roof of the lateral semicircular canal, the muscle fibres at the insertion of the levator operculi ossify and fuse with the perichondrial lamella. The articular surface for the hyomandibular ossifies later.

In the 32 mm. *Amiurus*, the two elements described by Schleip for *Salmo*, are present above the lateral semicircular canal. The dermal ossification contains the lateral line canal ossification and is partly fused with the perichondrial lamella (Fig. 31). Toward the middle line of the cranium the inner end of the dermal ossification is separated from the cartilage of the otic capsule by fibrous connective tissue and connects by suture with another dermal ossification which forms the margin of the median posterior fontanelle (Fig. 3). By fusion with the otic perichondrial ossification (Fig. 31), the dermal ossification loses its identity as a discrete ossification, as does the squamosal element of man when it fuses with the underlying periotic bones. Despite the fact that it is not related to an otic ossicle, I think that this dermal ossification overlying the roof of the lateral semicircular canal of *Amiurus* is the homologue of the mammalian squamosal. This homology however, does not apply to any other part of the compound bone. The perichondrial ossifications are formed around a center of ossification peculiar to fishes and called by Parker (1873), the pterotic ossification. As in *Salmo*, the fibres at the dorsal end of the levator operculi muscle have ossified and form a crest connected to the outer perichondrial lamella and extending posteriorly above the hyomandibular. At the posterior end of the roof of the lateral semicircular canal, the ventral arm of the post-temporal ossification projects in beneath this crest (Fig. 3). The dorsal arm of the same ossification lies behind the crest of the epiotic ossification and above the perichondrial ossification on the outer surface of the roof of the posterior semicircular canal.

Posterior to the hyomandibular articular surface on the dorso-lateral face of the lateral semicircular canal wall, the opercular-mandibular lateral line canal ends at this stage. The lateral line canal in the squamosal sends down a tubule which opens immediately above the dorsal end of the opercular-mandibular canal and eventually unites with it as in the adult (Fig. 11). The canal passes from the squamosal into the post-temporal, but before entering the latter, the osseous canal enclosing the sensory canal, is independent (Fig. 3). There is also a short interval between the end of this canal ossification and the post-temporal, where the canal lies unenclosed in connective tissue.

In certain regions of the roof of the lateral semicircular canal, the cartilage has been resorbed, as the foramina left in the chondrocranial roof show (Fig. 3), and the dermal ossification together with the lateral line ossification forms the protecting roof. The cavum of the inner ear and that of the lateral osseous canal are separated by the perichondrial ossification of the inner surface of the resorbed wall (Fig. 31). In the 60 mm. stage, endochondrial ossification has appeared in some regions between inner and outer lamellae, so that the space formerly occupied by cartilage is now filled with osseous trabeculae, just as in the more anterior sphenotic region (Fig. 33). Toward the posterior end of the roof of the lateral semicircular canal, the perichondrial lamellae, both inner and outer, are present in the 32 mm. stage (Fig. 31).

The ossification of this region of *Amiurus* agrees with the descriptions of Schleip, Gaupp, Allis and others for the teleosts, but the name squamosal employed by them should not be used alone in naming this compound bone. A squamosal element is present, but the name cannot be applied to the whole bone, as it consists of a pterotic ossification with a squamosal element added (Fig. 31); it is more like, but not completely in agreement with the mammalian temporal.

The epiotic ossification (Figs. 3, 38), or the ossification around the dorso-posterior wall of the posterior semicircular canal, has been described by various authors as a perichondrial ossification. In the teleosts it is connected to the post-temporal ossification of the shoulder girdle by a ligament which ossifies in connexion with the outer perichondrial lamella. In places the cartilage is resorbed and the lamellae form the wall. It is homologous with one of the centers of ossification of the periotic cartilage of man.

This ossification is well developed in the 32 mm. *Amiurus*. Inner and outer osseous lamellae appear in the perichondrium of the dorso-lateral and posterior walls of the posterior semicircular canal. The ligament which connects the outer lamella to the post-temporal is just beginning to ossify (Fig. 38). The posterior dorsal part of the cavum for the posterior semicircular canal is filled with osseous trabeculae continuous with the inner lamella. There is no resorption of cartilage at this stage.

At the 60 mm. stage, the perichondrial lamellae are much thicker and cover more surface. The outer lamella has extended ventrally on the wall of the semicircular canal so that it meets the ascending exoccipital ossification. Near the anterior end of the posterior semicircular canal roof, the cartilage has disappeared and the outer lamella alone forms the wall.

*The occipital region.* This part of the cranium has grown considerably since the condition described for the 10 mm. larva. The cartilage forming the posterior margin of the posterior fontanelle has grown forward and, together with the medial edges of the otic capsules, forms the synotic tectum (Fig. 3). There are ossifications on both the inner and outer perichondria of this tectum, which have been described in other teleosts as the centre of the supraoccipital

bone. The morphology of this bone will be discussed under the adult description. Sagemehl (1891) claims that the supraoccipital of the adult is a new formation in the teleosts and is not found in the ganoids nor in the dipnoi, and that it is the result of a fusion of one or more vertebra with the protometameric cranium.

In *Salmo* (Schleip), paired parietalia are present and form discrete bones in the adult. In the larva they develop as dermal sheets dorsal to the otic capsules, fused anteriorly to the frontals, laterally to the squamosal element of the squamoso-pterotic, and medially to the anterior ends of the supraoccipital. They are separated from the cartilage of the otic capsule by fibrous connective tissue.

In *Amiurus* there are a pair of such dermal ossifications in the same region and having the same histological relations. These ossifications are fused medially with the perichondrial ossification on the margin of the posterior fontanelle (Fig. 34). Despite this fusion with the perichondrial ossification, these dermal ossifications are comparable to those of the parietalia in the developing *Salmo*. The adult cranium shows that these ossifications do not persist as discrete bones as they do in *Salmo* and other teleosts. Laterally they are connected with the squamosal by a thin stroma of fibrous connective cells (Fig. 3) and anteriorly are continuous with the frontalia (Fig. 3). They have no lateral line relationships.

The details of the developing supraoccipital ossification have been described by Schleip for the salmon. The main part of this ossification, according to this author, develops as inner and outer lamellae in the perichondrium of the synotic tectum. The median dorsal fibrous septum between the dorso-lateral muscles of the two sides of the body ossifies as a vertical osseous plate above the outer lamella and connected with it. It supports at its dorsal end a horizontal osseous sheet developed from the fibrous connective tissue between the muscles and the corium. He calls it the spina occipitis. Both inner and outer osseous lamellae extend forward on the margins of the fontanelle anterior to the synotic tectum and are connected with each other by a transverse fibrous sheet which later ossifies and forms the roof of the cranium in this region. Schleip maintains that this fibrous sheet was originally part of the chondrocranium whose ontogenetic history has become shortened.

In *Amiurus*, at the 32 mm. stage, the synotic tectum, as remarked above, is well developed. Inner and outer osseous lamellae are present in its perichondrium (Fig. 34). The ramus lateralis accessorius facialis and the jugular vein of each side are enclosed in a canal formed by this perichondrial ossification along the posterior margin of the fontanelle. This canal has its anterior end at that point where the nerve and vein extend dorsally from the brain, medial to the anterior end of the posterior semicircular canal. In the 10 mm. larva, this nerve and vein lie dorsal to the cartilage of the roof of the posterior semicircular canal. After that stage was passed the cartilage below the nerve

and vein has been resorbed and the perichondrial osseous lamella forms the floor of the canal in which they lie in the 32 mm. stage. The outer perichondrial ossification, together with the parietal ossification, forms the roof of the canal, while the cartilage of the synotic tectum forms its lateral walls.

Near the anterior end of the otic capsules, the perichondrial lamellae on the margins of the fontanelle interdigitate with the frontalia (Fig. 3). There is no lateral line ossification anywhere near the vicinity of the developing supraoccipital.

The spina occipitis element of the supraoccipital is developed from the ossification of the fibrous sheet between the dorsal anterior muscle segments and the connective tissue on the dorsal surface of these (Fig. 29), as in Salmo. Near the anterior end of the spina occipitis the dorsal dermal sheet is very broad and extends laterally above the anterior ends of the body muscles (Fig. 3). The connexion of this sheet with the outer perichondrial lamella is affected by numerous osseous trabeculae. The interval between the dermal sheet and the perichondrial ossification gradually becomes greater more posteriorly, and the trabeculae become limited to the apex of the occipital arch (Fig. 29).

The dorso-lateral sides of the occipital arch are embraced by a pair of osseous plates, posterior to the otic capsules and separate from the cartilage of the arch by fibrous connective tissue (Fig. 29). These plates enclose the neural arch of the third vertebra which ensheathes the posterior end of the occipital arch and are fused with the perichondrium of the former farther posteriorly. These may be the representatives of an ossification comparable to the proatlas of the reptiles.

*The maxillary region.* The premaxillary ossification lies in the same place as in the younger stage and differs only in its extent and in the greater number of teeth attached to the ventral surface (Fig. 4). The maxillary ossification is larger, and, as before, forms a case for the proximal end of the maxillary barbel cartilage. It is attached to the lateral surface of the palatine cartilage, (Fig. 4).

*Mandibular and suspensorial apparatus.* The palatine cartilage has persisted to a great extent, but there are regions anterior to its articulation with the ectethmoid where the perichondrium has ossified and small osseous processes of bone project from its periphery (Fig. 22). The anterior end of the cartilage is large and spherical, tapering posteriorly as in the younger stage (Fig. 4), and it is flattest at the place of contact with the ectethmoid process. A small knob of cartilage projects posteriorly from its anterior dorsal surface, to serve as a support for the beginnings of the lacrimal (Fig. 3). Posterior to the articular surface the palatine is held in position by a pair of muscles which extend from the ethmoid cartilage and are fastened to its ventral and dorsal surfaces respectively (Fig. 39). Schleip ('03) says that the palatine of the salmon and trout is a mixed bone and that it has both perichondrial and dermal ele-

ments entering into its composition. In the ganoids (Van Wijhe, 1882) there is a dermopalatine below the perichondrial autopalatine which, in *Spatularia* (*Polyodon*), is attached to the maxillary and in *Polypterus* to the ectopterygoid. No such bone or ossification occurs in *Amiurus*.

The pterygoquadrate cartilage is larger than in the younger stage and the pterygoid part forms the middle of an osseous sheet, which extends ventrally beneath the cranium and posteriorly below, medial to Meckel's cartilage (Fig. 5). This is the centre of the metapterygoid bone of the adult. The quadrate is ossified along its ventral margin and is continuous dorsally with the ossification around the ventral and anterior edges of the hyomandibular cartilage. The posterior edge of this ossification is raised slightly above the surrounding parts and encloses the superior part of the operculo-mandibular canal of the lateral line; it is the anlage of the preopercular bone which has these relations in the adult. The hyomandibular branch of the facialis issues through this ossification, immediately below the anterior edge of the hyomandibular cartilage. This whole region, except for the preopercular part, was preformed in cartilage in the younger stage, the latter part having become secondarily attached to the perichondrial ossification of the hyomandibular. The dorsal part of the hyomandibular cartilage persists and abuts against the lateral surface of the otic capsule in the same region as in the younger stage. The opercular knob on its posterior face is larger and furnishes articulation for the thin plate-like operculum (Fig. 5). The interoperculum lies at the ventral end of the latter, between it and the mandible.

The centre of the dentary bone appears on the lateral surface of Meckel's cartilage and at this stage is distinct from the cartilage (Fig. 25). Teeth are attached to the dorsal anterior surface of this ossification (Fig. 5). A lateral line ossification, which has arisen independently around the mandibular lateral line canal, is attached to its ventral surface and is perforated for passage of dermal tubules of the canal. Meckel's cartilage lies in a groove on the medial surface of this ossification. In the 60 mm. stage perichondrial ossification has appeared on the surface of the cartilage and is connected by osseous trabeculae with the dermodentary (Fig. 24). The cartilage at the anterior end of the jaw has been resorbed where the symphysis takes place and the ossification here, although usually fused with the dentary, has been compared by Van Wijhe to the mento-Meckelian bone in the ganoids. He says (1882) that this bone is distinct in *Polypterus* and *Amia* and that it is fused with the dentary in *Lepidosteus*. The dentary is present as a dermal bone only, in all of these forms. In *Salmo* (Schleip 1903) the dentary is made up of the same elements as in *Amiurus*. McMurich (1884b) recognized the elements which make up this bone in *Amiurus*.

The posterior end of Meckel's cartilage is covered by a perichondrial ossification, the centre of the articulare, which furnishes the surface for articulation with the quadrate. There is no independent ossification on the top of the



coronoid process corresponding to the autocoronoid of the ganoids (Van Wijhe, 1882). The angulare, or possibly the goniale, is represented by a small dermal ossified sheet ventral to the articulare. The lateral line canal leaves the dentary at its posterior end and extends ventral to the articulare and thence into the preopercular. In the ganoids the articulare is formed in the same manner as in *Amiurus* and has been called the autarticulare (Van Wijhe, 1882), but has a dermarticulare attached to it as an independent bone. In *Salmo* (Gaupp, 1906) the articulare is developed from two such elements, the latter containing the lateral line canal.

#### THE ADULT SKULL

McMurrich (1884) has described the cranium of the adult *Amiurus catus*, but his description and figures are incomplete and could not be used to supplement the points brought out in the first part of this paper. Other authors have made passing reference to the cranium of the Siluroids in general but none of them give a specific description of the osteology of any one species from the point of view adopted in this paper. Pollard (1895) gives several figures of the chondrocrania of some of the South American forms, with a brief general description of each, but no reference is made to their osteology. Herrick (1901) notices the topographical relations of the cranial bones of *Amiurus melas* in his discussion of the cranial nerves.

The cranium of the adult *Amiurus nebulosus* (*catus*) is more depressed and flattened than in the later larval stages. The ossifications laid down in the 32 mm. stage have invaded and replaced the cartilage in many parts. There is however, more cartilage remaining in the adult cranium than McMurrich (1884b) noted (p. 271): "Very little cartilage remains in the skull, the anterior portion of the ethmoidal cartilage alone remaining unossified." I find considerable cartilage present in the floor of the cranium posterior to the ethmoid region, between the otic capsules (Fig. 7), and in the walls of the semicircular canals. The posterior instead of the anterior part of the ethmoid region remains unossified as the internasal septum, and will be discussed with the supraethmoid bone.

The fontanelles of the roof are well described by McMurrich (p. 270). My description of them is more complete, as I have traced their formation from the younger stages and have followed the changes which have resulted in their restriction to the median region of the roof. The ossification which divides them into anterior and posterior fontanelles (Fig. 10), is formed around the epiphysial bar of the larval chondrocranium. Most of the bones of the dorsal surface of the cranium have a delicate sculpturing.

*The supraethmoid* (Figs. 6, 7, 10). This bone in *Amiurus* has been described by McMurrich (1884b), as the 'mesethmoid.' This name implies that the bone is developed within the ethmoid cartilage and not around it, as has been shown for the larval stages. In development, the bone arises from der-

mal and perichondrial ossifications. Allis (1910) has described the bone in this region of the Loricati as the 'supraethmoid'; Sagemehl (1884), a dermal bone in this region of *Amia* as the 'ethmoid'; Parker (1873) and Gaupp (1906) as the 'supraethmoidale,' in *Salmo*; and Gegenbaur (1878), as the 'ethmoideum medium,' in *Alepocephalus*. These various terms have been used to a greater or less extent by other investigators, without regard to the significance of the terminology used. I have used the terminology of Parker and Gaupp as it applies better to the bone in *Amiurus* than any of the other terms. Very few of the authors who describe the morphological relations of the bone have studied its development and earlier histological relations; those who have agree that, in most teleosts, this bone has two parts, dermal and perichondrial, respectively. In the ganoids, as represented by *Amia* (Sagemehl, 1884), the dermal element alone is present in the same position as that element in the teleosts. A comparison of *Amiurus* and *Amia* will be made later, after this bone in the former animal has been discussed. In some of the teleosts, the dorsal surface of this bone is very rugose and is covered with numerous spines. It is usually an unpaired bone, its diverging posterior edges interdigitating with the frontals.

In *Amiurus*, the supraethmoid is the terminal bone on the dorsal surface of the cranium (Fig. 10). Its dorsal surface is slightly concave toward the posterior margin where it forms the anterior margin of the anterior fontanelle (*a.f.*). There are no spines on its dorsal surface, which is covered with fine ridges radiating from the margin of a notch (*eth. n.*) in the median anterior edge of the bone. Lateral to this notch, which is semicircular in outline, the bone sends out two cornua, which form the antero-lateral edges of the bone, and are the result of growth anteriorly of dorsal and ventral dermal ossifications from the ethmoid cornua of the 32 mm. larva, at which stage the ossifications are not present, although they begin to develop in the 60 mm. stage. They fuse with each other anteriorly, forming the sharp anterior margin of the cranium and the anterior wall of the nasal fossa (*n.f.*). They enclose a space which extends toward the middle line as far as the perichondrial part of the bone (Fig. 7). The ventral sheet extends posteriorly on the ventral surface of the cranium for a very short distance (Figs. 6, 16). The extent of this ossification can be seen only by removal of the premaxillary bones, which are closely connected to its ventral surface by tough fibrous ligamentous tissue. The anterior margin of the vomer (*Vo.*) interdigitates with the ventral ossification, and upon removal of it, several spicules from the parasphenoid (Fig. 7 *ps.*), are also visible in contact with it.

The parasphenoid lies ventral to a broad surface of cartilage (*eth.*) which forms the posterior ventral floor of the internasal septum. In a longitudinal section through this region (Fig. 7) the relations of the ossifications to the cartilage are well brought out. The ossification, which in the 32 mm. stage forms a perichondrial layer in contact with the superficial dermal ossification, has

now penetrated the cartilage, which in the adult is entirely ossified in the anterior region. A transverse section through this region of the 60 mm. stage shows the beginning of the invasion of the cartilage by the bone, both dorsally and ventrally. The posterior margin of the internasal septum persists as cartilage (Fig. 7). It extends dorsally on the ventral surface of the dermal ossification as far as the interdigitation of this with the frontals. Ventrally it extends as the floor of the cavum cranii as far posteriorly as the orbitosphenoid (OS.). This is opposed to McMurrich's statement that the anterior end of the ethmoid plate of the larva remains unossified in the adult.

Anterior to the olfactory foramen, the supraethmoid and the ectethmoids of each side interdigitate in the wall of the nasal fossa. Comparison with the condition of this region in the 32 mm. larva (Fig. 3), shows that the ossifications of the supraethmoid and the ectethmoid are perichondrial, and are developed on the outer wall of the massive internasal septum. The jagged suture between the two bones extends dorso-posteriorly as far as the frontal-supraethmoid suture (Fig. 10) and ventrally as far as the vomerosupraethmoid suture (Fig. 6). The ectethmoids are in contact with the edges of the ventral surface of the supraethmoid and curve posteriorly from it on the surface of the ethmoid cartilage (Fig. 16). McMurrich (1884) says that the supraethmoid interdigitates posteriorly with the orbitosphenoid, and, as my figures show, this is effected by posteriorly extending spicules of the perichondrial ossification on the ventral surface of the ethmoid cartilage, as the main parts of the two bones under consideration, are widely separate (Fig. 16).

Comparison of the median section of this region of *Amiurus*, with that of *Amia*, (Sagemehl, 1884), shows several important differences. The solid cartilage characteristic of the ganoid internasal region is present in *Amia*, and there are no ossifications in it. The ethmoid is a dermal ossification and lies near the dorsal anterior end of the massive internasal septum. The cartilage beneath this ossification continues posteriorly as the solid tegmen cranii, whereas in *Amiurus*, the posterior margin of the internasal cartilage ends dorsally at the anterior end of the frontals. There is no perichondrial ossification in this region in *Amia*. The premaxillary bone abuts against the ventral surface of the anterior end of the cartilage, there being no intermediate ossification, such as is found in *Amiurus*; nor does the vomer come in contact with the ethmoid, but, since the ethmoid of *Amia* is comparable to the dorsal part of the dermo-supraethmoid of *Amiurus*, this condition is not remarkable. The ossifications surrounding the ethmoid plate of *Amiurus* have invaded the cartilage, while all the ossifications in this region of *Amia* are dermal. That the cartilage has not entirely ossified in *Amiurus* is evidence that it has advanced but little farther in its osseous development than has *Amia*.

In the Characinidae (Sagemehl, 1885)—another of the lower teleost families, which in American piscine classification (Gregory, 1907), is closely allied to the siluroids as an offshoot from the lower branches of the teleost stock—

the ethmoid region is comparable, to a great degree, with the condition of *Amiurus*. The internasal septum, except in some of the very lowest genera of the family, has the same relations as in *Amiurus*. The vomer is usually more massive and extends ventrally in between the ethmoid (Sagemehl) and the cartilage. According to Sagemehl, the ethmoid has a double origin as in *Amiurus*, the amount of ossification varying from the Amioid condition to complete ossification of the internasal cartilage. In speaking of the ventral extent of the ethmoid in this group, he hoped that further investigations would justify his conclusions that such a condition did exist in other teleosts.

In the Cyprinoids (Sagemehl, 1891), there is more or less invasion of the cartilage of the internasal septum by bone, but none of the species have proceeded as far as *Amiurus* in this respect. In this family the ossification around the ethmoid cartilage has extended on to the ventral surface and is here in contact with the vomer. Concerning this region Sagemehl says: "In Folge dieses Verhaltens können wir bei Cyprinoiden an jedem Ethmoid zwei Theile unterscheiden: eine dünne Knochenplatte, die annähernd dem ursprünglichen Deckknochen entspricht und die lateral die Nasengrube überdacht, und eine von dieser Platte nach unten absteigende mehr oder weniger breite, aus spongioser Knochensubstanz bestehende, vertikal gestellte knöcherne Wand, welche die beiden Nasengruben von einander scheidet, und die durch Knorpelsubstitution entstanden ist."

This condition is also true of *Amiurus* as shown in an earlier part of the discussion. Hence the degree of ossification in the ethmoid region of the Characinidae, Cyprinidae and Siluridae affords another factor for grouping them together.

Of the Loricati (Allis, 1910), *Trigla* has a part of the internasal septum invaded by bone, but in none does the dorsal ossification, either dermal or perichondrial, extend over the anterior end of the cranium. In *Salmo* and most of the other teleosts, the ossification is entirely dermal and has no perichondrial element connected with it, repeating the condition found in *Amia*. From the above comparisons I think that, of all the lower teleosts, *Amiurus* has the largest amount of ossification in this region and the steps in the formation of it show that it is both dermal and perichondrial in origin. The former is the first of the two ossifications to appear.

*The ectethmoids.* Each of these is developed around the ectethmoid process of either side. In the discussion of this region of the younger forms, the changes which have taken place have been described and the beginning of ossification in the 32 mm. larva has been noted. Perichondrial ossification had just begun at that stage, while the large membranous sheet attached to the lateral edge of the cartilaginous ectethmoid process had already ossified and extended posteriorly above the orbit. In the 60 mm. larva, perichondrial ossifications have appeared on both the dorsal and ventral surfaces of the cartilage which

forms the floor of the nasal process and the basal part of the process. The ossification of the dorsal surface unites with a descending perichondrial wall from the ventral surface of the roof of the internasal septum and forms the olfactory canal. Thus, in the adult, there is no cartilaginous floor in the nasal fossa, but it is formed by the premaxillary bone and tough connective tissue. In spite of all the perichondrial ossification which has taken place in this region, the articular surface for the palatine and a small strip ventral to it remain uncovered (Fig. 16). This cartilage lies between dorsal and ventral ossifications of the ectethmoid anteriorly, but posterior to the articular surface these parts unite (Fig. 16). The ventral ossification interdigitates anteriorly with the vomer, and, at the very edge of the cranium, with the supraethmoid (Fig. 6). Further contact between the ventral ossification of the ectethmoid and that of the supraethmoid is prevented by a wide expanse of cartilage visible upon removal of the vomer (Fig. 16). This figure also shows the distance between the ectethmoids of the two sides and the very regular edge that each has. They are also separated from the orbitosphenoid (OS.) by cartilage.

Posteriorly and above, the dermal ossification attached to the margin of the bone is indistinguishably fused with the perichondrial ossification surrounding the foramen orbito-nasale (Fig. 10). This dermal ossification is a very pronounced process projecting at right angles from the cranial wall. Its medial end is continuous with that part of the bone which, with the orbitosphenoid, forms the upper and lower margins of the orbital foramen (Fig. 20). These are the main features that distinguish the bone. Its dorsal surface is covered with small ridges which radiate from the center. There are also numerous nerve foramina for twigs of the ophthalmicus superficialis trigemini, but none of these are connected with a lateral line canal as McMurrich (1884b) stated, because no such canal is included in the ectethmoid. The posterior margin of the lateral process is continuous with a similar one on the margin of the frontal of the same side. The inner surface of the bone is covered with a thin layer of cartilage (Fig. 7).

Cuvier (1828) called this bone the 'frontal anterieur' and described it briefly in the perch. In his diagnosis, he said that it enclosed the olfactory nerve, was not entirely ossified, and had an articular surface for the palatine and maxillary bones. The suborbitals were attached to its lateral surface by ligamentous tissue. Except for the connexion with the maxillary, this description would apply in a very general way to the ectethmoid as described in this paper. Stannius (1854) used the terminology of Cuvier in describing this bone in the teleosts, and stated that it was one of the marginal bones of the first and second head segments.

Huxley (1864) remarked this bone as a development around the ectethmoid process in *Esox*, and, though calling the ossification, the prefrontal, he stated that it was comparable to the lateral mass ossification of the ethmoid bone of human anatomy. Vrolik (1873) followed Huxley in using this name. Its

synonymy may be found, in common with that of the other cranial bones, in tables given by Owen (1848), Vrolik (1873), and Starks (1901). Vrolik very briefly describes this bone as a 'perichondrostische' ossification, that is, what is here called a dermal ossification. It is figured for the carp, *Silurus* and other teleosts, but he does not discuss it further.

In the Cyprinoids (Sagemehl, 1891) it encloses the olfactory nerve and the ophthalmic branch of the trigeminus, has an articular facet for the palatine, and is called the prefrontal. It projects very abruptly from the lateral surface of the cranium, separating the nasal fossa and the orbit. Its developmental relations are not discussed. These same relations also hold true for the Characinidae as described by the same author (1885).

Gegenbaur (1878) calls this bone the 'ethmoide laterale' or 'praefrontale' in *Alepocephalus*. He distinguishes two parts, a lateral and a medial, the latter is developed from the ethmoid cartilage and forms the inner wall of the olfactory canal. He claims that the sculpturing on the dorsal surface is arranged concentrically and that the ridges represent lines of growth. The bone does not have the extensive articulation that it has in *Amiurus*, but is limited to the cap of the ectethmoid process.

McMurrich (1884b) made two statements concerning this bone in *Amiurus*, which contradict each other. In one place (p. 277) he says that the upper surface of the bone is very irregular and has numerous foramina connected with the mucous canal system. Farther along in the same paper (p. 280), he says that there is no connexion between the ectethmoid and the mucous canal lying dorsal to it. If the first statement were qualified to mean nerve foramina, as I think he really means, there would be no confusion in interpreting his statement. Since there are canal foramina in some of the bones of this region, this qualifying statement should be made.

Gaupp (1906), in remarking upon the development of this bone in *Salmo*, calls it the 'pleurethmoidale,' introducing an entirely unnecessary term. If one standard of nomenclature is to be adopted in comparative osteology, it should be adhered to as far as possible. Anyone reading Gaupp's papers is at once struck by the flood of new and unnecessary terms throughout all of them. According to this investigator, the ectethmoid of the adult *Salmo* is a true perichondrial ossification formed around the planum antorbitale (ectethmoid process). The adult condition is the result of endochondrification and resorption, with an added ossification formed by the ligament connecting it to the palatine. The bone includes the ophthalmic branch of the trigeminus, and the anterior ossicle of the infraorbital chain of bones is attached to its lateral surface.

Allis' (1910) description of the development of this bone in the mail-cheeked fishes (*Loricati*) is given earlier in the paper, but we can compare the adult bones at this time. As was stated previously, both have perichondrial and dermal elements, although Allis claims that the latter is perichondria

rather than dermal. The olfactory nerve issues through this bone in the mail-cheeked fishes, and in *Amiurus*, the olfactory tract. Both have a foramen for the passage anteriorly of the ophthalmicus superficialis trigemini and a facet for articulation with the palatine.

*The nasals.* In the 32 mm. stage, the only ossifications in the roof of the nasal fossa of each side were those developed around the anterior ends of the supraorbital and suborbital lateral line canals. At that stage they were narrow and tubular, the more medial ossification enclosed the supraorbital and the more lateral the suborbital canal. They were connected to the surrounding bones by ligamentous tissue, there being no contact of ossifications. In the adult, the more medial of the two bones is recognized as the nasal and the more lateral as the lacrimal. The nasal (Fig. 15) is flat and covers most of the fossa roof, its concave antero-lateral margin forming the median margin of the anterior naris. The lateral line canal occupies a very limited space on the longitudinal median dorsal surface of the bone. This canal opens anteriorly by two pores, one at the tip of the bone (Fig. 11), and the other on the latero-anterior margin, posterior to the anterior naris. Posteriorly, the lateral line canal passes from the narrow posterior tip of the bone and proceeds through a mass of connective tissue before entering the anterior end of the frontal (*fr.*). The flat and scale-like appearance of the bone is the result of ossification of part of the fibrous connective tissue below the lateral line canal ossification. In outline the bone is suggestive of the nasal of *Amia* (Sagemehl, 1884), but it is not nearly as massive nor does it meet its fellow of the opposite side. The enclosed lateral line canal does not connect with that of the other side within the ethmoid as it does in *Amia*. The nasal of the Characinidae (Sagemehl, 1885) is more like that of *Amia*, and comes in contact with the ethmoid cartilage as in the latter, but not in *Amiurus*. The Cyprinoid nasal is more nearly like that of *Amiurus* than of *Amia* or the Characinids. In *Salmo*, (Schleip, 1903) the nasal develops in contact with the ethmoid cartilage and encloses a lateral line canal. In *Gasterosteus* (Swinnerton, 1902), this bone is very large and intimately connected with the ethmoid cartilage; it extends on to the ventral surface of the cranium after forming the roof of the nasal fossa, but the presence of a lateral line canal within it is not mentioned.

In the Amphibia, Reptilia, Aves, and Mammalia, the nasal bone occurs as a dermal ossification on the roof of the nasal capsule. In some mammals the cartilage of the capsule beneath this bone disappears, and a condition comparable to that of *Amiurus* results. The teleostean nasal bone is comparable, then, in a certain degree with the nasal of the higher groups. In nearly all of the teleosts however, this bone contains a lateral line canal ossification on its dorsal surface. In *Amiurus* the bone is isolated, but in most of the other forms it connects to a greater or less degree by suture with the surrounding bones.

*The lacrimals.* A single lacrimal on each side of the head forms the lateral roof of the nasal fossa (Fig. 15). Each is very small and narrow and contains

the anterior end of the suborbital lateral line canal of its side. The most anterior dermal tubule of the canal issues from the bone through its dorso-medial edge (Fig. 11). From the small central part of the bone four processes radiate, two anterior and two posterior. The antero-lateral process is slender and curves around the external margin of the anterior naris. The anterior end of the suborbital canal, after leaving the main part of the bone at the proximal end of this process, proceeds immediately to the external surface of the head. The process is closely connected by ligament to the maxillary and premaxillary bones, and to the ethmoid cornu of the supraethmoid bone.

The median anterior process of the lacrimal projects toward the middle line of the fossa roof, posterior to the anterior naris. It contains the first dermal tubule of the suborbital lateral line canal, the pore of which lies lateral to the pore of the first dermal tubule of the supraorbital canal, posterior to the margin of the anterior naris (Fig. 11).

The elongate median posterior process extends posteriorly toward the anterior face of the ectethmoid bone. It lacks a lateral line canal element. The anterior ossicle of the infraorbital series of lateral line canal bones (Fig. 15) is connected with its ventral margin by ligament. The lateral posterior process of the lacrimal lies external to the first suborbital bone, so that the suborbital lateral line canal enters the posterior margin of the lacrimal between the posterior processes. After giving off the dermal tubule described above, the canal ends by the passing to the exterior. There is one sense organ, the most anterior of the suborbital lateral line canal, contained within the lacrimal bone. The nasal bone encloses the most anterior sense organ of the supra-orbital canal.

The older writers—Cuvier, Stannius, Hallman, Wagner, Huxley and others—recognized the lacrimal bone as the anterior element of the suborbital or infraorbital series. In most of the forms studied it was the largest and gradually came to have a greater morphological significance than the more posterior elements of the series. It contains a part of the suborbital lateral line canal in most teleosts and in *Amia*, and is usually related to the roof of the nasal organ. Where its development has been studied (Schleip, 1903), it has been found to arise primarily as an ossification developed in connexion with a lateral line sense organ, and later has an osseous base formed from surrounding connective tissue. In *Amiurus*, as noted above, the lateral line element is the first to appear and the dermal part does not ossify until much later. I am satisfied that this bone has two parts as Schleip has stated, and that the dermal part may be homologized to the lacrimal bone of the higher groups. As the lateral line canal is associated with those forms which live in the water, so is the lacrimal canal found in those animals which pass most of their lives in the air. In both cases the bone develops lateral to and usually dorsal to the nasal organ and is a dermal ossification. It may have more or less connexion with the surrounding bones—nasal, maxillary, premaxillary, supra-



ethmoid, and ectethmoid—and in some of the fishes with the vomer. Allis' (1898) criterion for the homology of the lacrimal is the inclusion within it of the anterior end of the suborbital canal. In comparing his work on *Amia* with that of McMurrich on *Amiurus*, he concluded that the antorbital of *Amia* was the homologue of the adnasal (lacrimal, Author) of *Amiurus*. Since however, this bone of *Amiurus* contains the anterior end of the suborbital canal it is the lacrimal and the antorbital of *Amia* is represented by the long antero-lateral process, which has fused with the lacrimal element as it has in some other teleosts.

*The frontals.* These are the most extensive and conspicuous bones on the dorsal surface of the cranium, forming most of the roof and part of the side walls of the cavum cranii (Fig. 10). The only point of suture between the two is in the region of the original epiphysial bar. Anterior and posterior to this suture they are separated from each other by two longitudinal fontanelles, the remnants of the more extensive ones of the younger stages. Each has a raised margin on the sides of these fontanelles, thus bounding a fossa which continues anteriorly as far as the supraethmoid and posteriorly on to the dorsal surface of the supraoccipital. This fossa is filled with connective tissue and nerve fibres, and a tough membrane is stretched the entire length of each of the fontanelles. Their restriction is caused by median growth of the frontals, a process noted in its incipience in the 32 mm. stage. Earlier, however, the posterior fontanelle extended between the anterior edges of the occipital arch, but the ossification in this region has grown forward and closed the extreme posterior end of the fontanelle.

Anteriorly, the frontals interdigitate with the median supraethmoid, which forms the anterior margin of the anterior fontanelle. This interdigitation lies above the orbito-nasal foramen and is continuous laterally with that between the ectethmoids and the frontals (Fig. 10). An oblique frontal ridge, along which the adductor mandibularis muscle has its origin, extends posteriorly across the dorsal surface of the frontal from the lateral posterior margin of the ectethmoid. The frontal ridge does not extend to the posterior end of the bone, but unites with the ridge which forms the margin of the median fossa. Behind the union of the two ridges a wing of bone extends laterally to interdigitate with the sphenotic. Anterior to the ridge the surface of the bone is sculptured in longitudinal lines, which run posteriorly toward the middle line of the cranium, parallel to the dorsal margin of the ridge and extending along its anterior face. Posterior to the frontal ridge the bone is comparatively smooth.

At the anterior end of the frontal ridge the suborbital lateral line canal enters the frontal bone from the postfrontal (Fig. 11). The two bones are not in contact with each other, so that the canal crosses the dorsal surface of the adductor mandibularis muscle before entering the frontal. A dermal tubule is given off from this part of the canal as it passes from the postfrontal to the frontal.

The frontal bone extends down into the wall of the orbit, externally connecting by suture with the orbito- and alisphenoid ossifications (Fig. 20). In the anterior part of the orbit it is separated from the ectethmoid bone by a small remnant of the fused alisphenoid-ectethmoid cartilage. Posteriorly it interdigitates with the anterior end of the sphenotic bone, above the alisphenoid. On the inner surface of the *cavum cranii*, the frontal descends in the cranial wall in front of and behind the line of suture between the two frontals, but immediately below the suture this downgrowth is limited by the dorsal parts of the ali- and orbitosphenoids. Anteriorly it overlaps the orbitosphenoid and continues as far forward as the cartilage which lines the *cavum* within the ectethmoid. Posteriorly it overlaps the alisphenoid, interdigitates with the anterior margin of the sphenotic and proceeds dorsally toward the middle line of the cranium to interdigitate with the supraoccipital.

There are many minute nerve foramina and canals in the frontal bone, but none of them reach the *cavum cranii*. The largest canal is that of the *ophthalmicus superficialis facialis*, which, after issuing from the alisphenoid, sends a branch along the dorsal median wall of the orbit and is enclosed within the frontal. It continues forward within the bone, sending small twigs dorsally into the bone to the lateral line organs contained within it and also clear through the bone to the integumental sense organs above (Fig. 10). Anteriorly, the nerve passes to the dorsal surface of the bone through a small foramen, just below the insertion of the connective tissue which connects frontal with nasal.

The supraorbital lateral line canal, which starts in the nasal bone, enters the anterior end of the frontal after passing through the connective tissue between the two bones. The anterior point of ingress of the canal lies just dorsal to the foramen for the passage of the ophthalmic branch of the *facialis*. From this point its course cannot be followed externally, but must be traced by following it through a series of transverse sections, (a 60 mm. specimen was used for this). There is one dermal tubule and pore anterior to the frontal ridge on the dorsal surface of the bone. As noted above, the suborbital canal enters the frontal at the anterior end of the frontal ridge. It anastomoses with the supraorbital canal beneath the ridge and a dermal tubule extends along the posterior face of the ridge from the supraorbital canal, just before their anastomosis. The canal formed by the anastomosis continues posteriorly from the middle of the frontal ridge and thence into the sphenotic bone (Fig. 11). There are three sense organs in the canal enclosed in the frontal at points shown in Figure 11. The first and third are followed by dermal tubules, but the second, which lies just anterior to the union of supraorbital and suborbital canals is not.

This bone of the adult is the result of the ossification of the membrane above the alisphenoid cartilage of the larva. In sections through the 60 mm. larva the fibrous connective tissue surrounding the ventral surface of this membrane have ossified and appear as lamellae capping the perichondrial ossification of the dorsal surface of the alisphenoid cartilage (Fig. 32). The ossifications of

the two sides of the head have fused around the epiphysial bar, and the cartilage within it has all but disappeared. None of this ossification connecting the frontals of the two sides is perichondrial. In the adult, the cartilage has entirely disappeared from the interior of the ossification (Fig. 7) surrounding the original epiphysial bar. Anterior to this bar the frontal is thin and solid, while behind, although just as solid, the bone is much thicker. The nerve foramina in the bone are later developments and are caused by the growth of osseous trabeculae around the nerve twigs and branches. The ossification around the lateral line canal has now become an integral part of the bone.

The older comparative anatomists homologue the frontals of the fishes with those in the higher animals and based their conclusions upon topographical rather than embryological relationships. As far back in the literature as I have gone, these bones have always been known as the frontalia with, perhaps, an added adjective to distinguish them from the anterior and posterior frontalia. In practically every teleost and most of the ganoids they are the largest bones on the dorsal surface of the cranium and are usually paired. Fontanelles like those of *Amiurus* were recognized in the teleosts by Cuvier and are again referred to by Stannius (1854). In *Amia* and most lower teleost families these fontanelles are absent and the frontals are connected by suture along their entire length.

In comparison with the frontals of *Amiurus* those of *Amia* show limitations of development ventrally and internally. They cover more of the dorsal surface of the cranium than those of *Amiurus*, but they take no part in the wall of the *cavum cranii*, being separated from it by the solid cartilaginous *tegmen cranii* (Sagemehl, 1884). They do not interdigitate anteriorly with the *supraethmoid* because of its limited development, but their relations to the nasal bones are comparable to those of *Amiurus*. In the orbital wall, the frontal of *Amia* is separated from the *orbitosphenoid* and *alisphenoid* ossifications by cartilage. Cartilage does not extend between the frontal and *ectethmoid* (*prefrontal*, Sagemehl) as in *Amiurus*.

In the *Characinidae* there is a mixture of the condition found in *Amia* and that of *Amiurus*. *Citharinus* (Sagemehl, 1885) approaches the *Amiurus* type of frontal development externally, but is more like *Amia* internally, in that more cartilage persists in the side walls and the roof of the cranium than in *Amiurus*. The epiphysial bar is not enclosed by the frontals, although they meet above it. *Sarcodaces* lacks the anterior fontanelle found in *Citharinus* and the posterior fontanelle lies more between the parietals than the frontals. Internally, there is less cartilage than in *Citharinus*, but the epiphysial bar remains unossified. The other families of the lower teleosts—*Mormyridae*, *Osteoglossidae*, *Clupeidae*, *Gymnarchidae* and others—have the frontals connected by suture as far back as the parietals which are highly developed in these forms. The internal relations of the frontals have not been described for

any of these lower teleosts and it would be interesting to find out how much cartilage remains beneath them.

In the Cyprinidae (Sagemehl, 1891), the frontals have relations which closely approach those of *Amiurus*, but the anterior fontanelle is always closed in those genera figured by Sagemehl. The epiphysial bar persists as cartilage in the adult, and the frontals have not extended beneath it as they have in *Amiurus*. In none of the forms thus far mentioned have I been able to find a frontal ridge for the adductor mandibularis muscle comparable to that in *Amiurus*. The postfrontal (sphenotic, auct.) never has the dorsal extent that it has in *Amiurus*, but is always overlapped by the posterior margin of the frontal.

In the Salmonidae, the frontals lie superficial to the tegmen cranii (Parker, 1872), as they do in *Esox* (Huxley, 1864) and take very little part in the formation of the orbital roof, probably because of the persistence of the cartilage in this region. Further discussion of the topographical relations of the frontals is unnecessary because the above shows that there is a general agreement in position throughout the whole group of teleosts.

The relations of the nerves to this bone were neglected by the older anatomists and not until Sagemehl's description of *Amia* were these studied. As in *Amiurus* twigs from the ophthalmicus superficialis facialis (Sagemehl's fifth) pass into the bone to innervate the sense organs of the lateral line canal. The Selachians have a series of foramina in this same region penetrating the supra-orbital cartilage (Gegenbaur, 1872; Wells, 1917). In the Characinidae the ophthalmic branch of the facialis has the same relations as in *Amia* and *Amiurus*. In *Amia* an anterior branch of it extends dorsally through the cartilage and frontal at the anterior end of the orbit. In the Characinidae, Cyprinidae and *Amiurus*, this branch passes to the dorsal surface of the cranium through the frontal alone. In *Amiurus* it lies free in the orbit in the younger stages and its enclosure within the frontal is accomplished by growth ventrally from the frontal of osseous spicules which finally enclose the nerve within a canal.

Von K  lliker (1850) was one of the first to work out the histological development of the frontals. Up to his time there was a controversy between those who thought that the bone was developed from membrane and therefore comparable throughout the whole vertebrate series, and those who held that in the Aves and Mammalia it was developed from cartilage. Reichert (1849) was responsible for the latter statement and von K  lliker took it upon himself to settle the controversy by histological and chemical analysis. The chemical analysis of the bone showed that it did not have a trace of the chondrin common to the bones developed from cartilage. As a result of his work he came to the conclusion that the frontal bone throughout all the groups was developed from dermal connective tissue and had nothing to do in development with the underlying cartilage. Subsequent researches on the development of the bone have borne out his statement. Gegenbaur (1864) and Hertwig (1876) both agree that originally the frontal bones were dermal scales which, in the course of

phylogenetic changes, have sunken to their present position and fused into a solid osseous mass. *Acipenser* typifies the indifferent stage where the scales have not yet formed bones.

The supraorbital lateral line canal is usually associated with the frontal bone in the ganoids and teleosts, and there are many or few pores on the dorsal surface of the bone connected with it. Vrolik (1873), in his general description and in the conclusions of his work on the development of the frontal bones of teleosts, states that the frontal bone is developed primarily to protect the canal. This has since been refuted by those who have worked out the developmental relations of the canal and the bone. The ossification around the canal is at first entirely separate from that of the main part of the frontal (Klaatsch, 1895, Schleip, 1903, and others). In *Amiurus*, as remarked earlier in this paper these have been noted as separate ossifications.

In brief, the frontal bones of the teleosts are paired ossifications arising from fibrous connective tissue. They may lie above a solid cartilaginous roof or they may form an integral part of the cranial roof. Anteriorly they usually interdigitate with the supraethmoids and the ectethmoids, and are separated from the nasal bones by a connective tissue bridge across which each supraorbital canal extends to enter the frontal. Posteriorly they usually interdigitate with the parietals, but in the Siluroids the parietals are not present as discrete ossifications, so they interdigitate with the supraoccipital. There is commonly a fontanelle between the posterior ends of the bones, and in *Amiurus* and some few of the Characinidae there is an anterior fontanelle as well. The frontals overlap the orbitosphenoid and alisphenoid bones in the wall of the orbit, both internally and externally in those forms where ossification has proceeded very far. They also contain foramina and canals for the passage of the ophthalmic branch of the facialis to the integumental sense organs on the dorsal surface of the head and to the lateral line canal organs within the supraorbital canal.

*The infraorbitals.* This series includes the lacrimal described above, and another group of bones which extend from the posterior margin of the lacrimal below the eye, so that the most postero-dorsal bone of the series, the postfrontal, is attached to the frontal ridge, posterior to and above the eye (Fig. 15). The whole series is made up of three suborbitals, two postorbitals, and the postfrontal. These bones enclose the infraorbital or suborbital lateral line canal and are developed primarily for its protection. None of the bones unites by suture to its neighbors, but connexion is effected by ligamentous tissue and the fascia enveloping the muscles of this region.

The three suborbitals are the most slender and reed-like of the entire series. They lie deeply embedded in the connective tissue anterior and posterior to the ectethmoid process, two being anterior to the process and the third just behind it. The first is the smallest of the trio and the second is next in size. Both of these have practically the same diameter as the enclosed lateral line canal.

None of the suborbitals are sculptured. The third suborbital lies below the eye and is nearer to the cutis than the other two. It lies above the fascia of the anterior fibres of the adductor mandibularis muscle.

The two postorbitals are broader than any of the suborbitals. The first curves around the posterior margin of the eye and is attached superiorly to the inferior end of the second postorbital. The latter is the largest and longest bone of the series and is slightly curved dorsally toward the anterior part of the orbit. Ridges run on the anterior surface of the bone parallel to the course of the enclosed canal. Both postorbitals are firmly embedded in the fascia of the adductor mandibularis and the dilator operculi muscles, some of their fibres having their origin along the ventral surface of these bones.

The most dorsal and posterior bone, the smallest of the series, is the postfrontal. It lies dorsal to the superior end of the second postorbital, and like it, is embedded in the muscle fascia. This bone is not as flat as the others, the posterior margin being grooved, the margin of the groove projecting dorsally. The posterior end of the suborbital canal, which passes through the other bones of the chain lies within this groove. The anterior face of the bone is sculptured. As remarked above, the postfrontal is connected with the frontal by ligamentous tissue.

The principal morphological feature of this series of bones is their relation to the suborbital lateral line canal. From the lacrimal bone this canal extends through the infraorbital chain into the frontal. As it passes from one bone to the other it lies within the connective tissue which joins the two bones, and at these points between the bones, from lacrimal to frontal, a dermal tubule extends from the main canal to the surface of the integument where it opens by a single pore. There are five of these dermal tubules and pores between the posterior end of the lacrimal and the junction of the suborbital canal with the supraorbital in the frontal bone. There is no tubule between the lacrimal and the first suborbital nor between the postfrontal and the frontal. There is a sense organ in each bone of the series (Fig. 11).

The development of these bones has been studied by Klaatsch (1895) and Schleip (1903). The former claims that all the bones develop from osteoblasts which proliferate below each sense organ of the developing system. He maintains that all the bone connected with a canal arises from these same osteoblasts. Schleip derives the lateral line containing element proper from these osteoblasts, but goes no further. Allis (1898) thinks that true dermal elements are present, comparable to those which give rise to such bones as the frontal, supraethmoid, and other dermal bones of the head. In the development of *Amiurus* the bones begin as Klaatsch and Schleip have stated, and in the 32 mm. stage the canals are enclosed in tubular bones, all of which are close to the periphery of the canal wall. The rest of the bone is developed from the ossification of the fascia in the immediate region of these tubular bones, but I have not been able to trace the derivation of the osteoblasts which cause the ossification.

The number and size of these bones vary in the different families of ganoids and teleosts, but their position with regard to the eye and their relation to the suborbital lateral line canal are constant. The older comparative anatomists recognized them as the suborbitalia, or frequently as the infraorbitalia, setting off the anterior bone of the series as the lacrimal on account of its size and relation to the nasal capsule: Van Wijhe (1882) remarked in a foot-note, that the developmental relation of these bones to the suborbital canal was a good character for homologizing the bones in the different groups. The nomenclature used in this paper is based upon that used by Allis (1898) in *Amia*. McMurrich (1884b) found six bones in the series in *Amiurus*, but did not differentiate nor make a detailed study of any of them. He says there are pores in these bones for the passage of more or fewer mucous canal tubules. In reality, there are no pores for the passage of such tubules because these leave the canals between the bones, issuing through the connective tissue in this region. Collinge (1895) has given a partial description of the relations of the suborbital lateral line canal to the infraorbital bones in *Amiurus catus*, and figures no tubules between the lacrimal bone and the junction of this canal with the supraorbital. Gegenbaur (1878) recognized seven elements in the infraorbital chain of *Alepocephalus rostratus*, the posterior bones being situated in the muscle fascia on the dorsal surface of the cheek muscles. A dermal tubule passed to the exterior between each bone, and in the first of the series, which is comparable to the main body of the lacrimal of *Amiurus* there were a number of tubules as in the same bone in *Amia*.

Allis (1898) called the last bone of the infraorbital series in *Amia*, the postfrontal, and justifies himself in so doing, by stating that the postfrontal never fuses with the underlying postorbital perichondrial ossification and always contains a part of the suborbital canal. He states that in some members of the Characinidae, and Cyprinidae, and in Scomber, in which the dilator operculi muscle lies on the dorsal surface of the cranium, this postfrontal lies above the muscle. The postfrontal of *Amiurus* fulfills all of these requirements and hence corresponds to the same bone in the groups mentioned.

According to this view the infraorbital chain of bones is comparable to the orbital ring of the Stegocephalans and Reptiles, in which there is usually a large lacrimal anterior to the eye, a zygomatic below the eye, followed by a postorbital, above which is a postfrontal. The fact that, although the zygomatic bone is a member of the maxillary series, it never bears teeth lends some support to the assumption that it is a lateral line bone rather than dental in origin. Most older authors homologized this ring of the fishes on purely topographical relationships, to the jugal arch of the reptiles, and Bojanus (1818) called them the ossa jugalia. Gaupp (1906) makes no statement concerning this homology. Cuvier first applied the name postfrontal in the fishes to that bone which is today recognized as the sphenotic, because he thought it was the homologue of the postfrontal of the Reptiles.

According to Allis (1898), the lacrimal of *Amia* is the homologue of the first suborbital of *Amiurus*. He regarded the adnasal of *Amiurus* as described by McMurrich (lacrimal, Auct.) as the homologue of the antorbital of *Amia*, justifying his statement by saying that Collinge says that many authors call the bone by that name. Since this bone in *Amiurus* contains the anterior end of the suborbital lateral line canal, I have called it the lacrimal, and it is possible that the long anterior lateral process may be the homologue of the antorbital of *Amia*. Merely because there are six infraorbitals in *Amiurus* and *Amia*, counting the lacrimal in the latter, but not in the former, it does not follow that the members of the series are numerically homologous from the anterior to the posterior end. The criterion for homology rests upon the relation of the bone to the nasal capsule and the part of the lateral line that it contains.

*The vomer.* This bone, broad, flat, and unpaired, lies near the anterior end of the ventral surface of the cranium. It is entirely superficial to the bones which invest the chondrocranium in this region and is covered by the skin of the roof of the mouth (Fig. 6). As McMurrich (1884b) said, the bone is nail-shaped, the head of the nail is represented by the broad anterior portion and the shaft by the posterior spicules. It lacks the anterior extension common to the vomer of most teleosts, and is limited in front by the supraethmoid. The serrate line of interdigitation between these two bones extends as far laterally on each side as the ventral end of the supraethmoid-ectethmoid interdigitation. The vomer is here separated from the margin of the descending ectethmoid by a cartilaginous plate which is continuous with the palatine articular surface. Postero-laterally each side of the vomer interdigitates with the anterior edge of the ventral portion of the ectethmoids. Internal to these edges the several spicules mentioned above extend posteriorly in a series of grooves on the ventral face of the parasphenoid. The bone does not articulate with the premaxillaries and it is firmly united with the parasphenoid. The ventral ossification of the supraethmoid extends beneath it, separating the anterior part from the chondrocranium, while the anterior end of the parasphenoid cuts it off behind from the orbitosphenoid (Fig. 7). The bone itself is very thin and some of the fascia for muscle fibres of the entopterygoid muscle are attached to the postero-dorsal margins. It has no teeth and none are developed in the roof of the mouth below it. The development of the bone has been described earlier in the paper.

Since Cuvier compared this bone in the fishes to the vomer of man, it has borne this name, although many arguments have been advanced for and against this view which I will not attempt to discuss here. As it is one of the most evident bones on the anterior ventral surface of the skull in all teleosts, there has been no confusion in describing its topography. In some of the lower teleosts—Scomber, Salmo, and the Loricati are among the best known



examples—the vomer bears teeth and some have thought that these were an integral part of the bone. Schleip (1903) has shown that in *Salmo* the vomer develops, as in *Amiurus*, from deep-lying connective tissue beneath the chondrocranium and that the teeth arise independently. In some of the Characiniidae and Cyprinidae, the vomer is intimately connected with the cartilage of the ethmoid plate. In all adult teleosts it is unpaired, although it may arise from paired parts as in *Esox* (Walther, 1882). In some it forms a cap on the anterior end of the ethmoid cartilage. In none of the forms described up to this time has a condition wholly similar to that in *Amiurus* been found. Its limitation to the ventral surface of the cranium is not the common type of development, as there are usually anterior or lateral processes projecting for articulation with the cranial bones of the dorsal surface.

*The orbitosphenoid.* This is a large unpaired bone forming the floor and side walls of the cranium between the orbital and optic foramina (Figs. 6, 7, 16, 20). It is visible externally in the wall of the orbit, overlapped dorsally by the frontal and interdigitating anteriorly with the ectethmoid in both the upper and lower margins of the orbital foramen. This part of the bone is only a thin lamella on the cartilage which persists in the side walls of the cranium and unites with a similar lamella on the internal surface of the cartilage in the margins of the foramen.

The anterior end of the alisphenoid bone extends down in front of the optic nerve so that the orbitosphenoid is limited to the ventro-anterior wall of the foramen. In the midventral margin of the foramen it interdigitates externally with a lateral process of the parasphenoid, and the line between them extends across the ventral surface of the cranium to the optic foramen of the other side. The immediate middle part of this interdigitation is visible only upon removal of the vomer and the anterior spicules of the parasphenoid (Fig. 16). The ventral anterior end of the orbitosphenoid is separated from the laterally lying ectethmoids by cartilage. The median anterior margin lies quite far posterior to the main part of the supraethmoid, but several spicules from the latter bone extend posteriorly to it along the dorsal surface of the parasphenoid (Figs. 7, 16). The interval between the main parts of the supraethmoid and the orbitosphenoid is occupied by the ethmoid cartilage.

There is a notch on each side of the bone in the orbital wall, just behind the orbital foramen, for the attachment of the pterygoid muscles (Fig. 20). The ventral wall of the notch continues posteriorly as far as the optic foramen and forms a shelf supporting the optic nerve. The whole ventral surface of the bone is roughened by fine lines. On the median ventral part of the bone, which is closely applied to the dorsal surface of the parasphenoid, the lines run longitudinally, and on the lateral parts in the orbital walls, they radiate from a center on each side (Fig. 16).

A longitudinal section through the cranium shows the relative extent and thickness of the orbitosphenoid (Fig. 7). The dorsal posterior surface of the

bone is overlapped by the suprasphenoid and the ventral, by the parasphenoid; suprasphenoid and parasphenoid bones fusing at the posterior margin of the bone. Anteriorly the orbitosphenoid thins out and passes gradually into the cartilage of the internasal septum. The middle part of the bone has entirely ossified, but the persistence of cartilage beneath the external lamellae of the lateral parts of the bone shows that ossification does not extend uniformly through all its parts. The frontal overlaps the dorsal margin of the bone in the cavum wall and in line with the epiphysial bar region the alisphenoid and orbitosphenoid meet above the optic foramen. Considerable cartilage remains in both of these bones in this region, but between this point and the anterior end, the part of the orbitosphenoid which forms the wall of the cavum is well ossified. Below the optic foramina the orbitosphenoid-suprasphenoid interdigitation continues from one side to the other within the cavum, marking the posterior limit of the orbitosphenoid as a lining bone of the cavum cranii (Fig. 7).

The developmental relations of the orbitosphenoid have been given for the 32 mm. stage (p. 52). The perichondrial ossifications in the wall of the cranium which now form an integral part of the bone were then just beginning. From the description just above, it is evident that there is considerable cartilage yet remaining within these osseous lamellae. The ledge on the external surface of the bone, between the orbital and optic foramina, is developed from connective tissue surrounding the ventral end of the alisphenoid cartilage and the trabecula cranii, and is intimately connected with the perichondrial ossifications of these cartilages (Fig. 3). The stout median part of the bone is developed from perichondrial ossifications which have fused with each other across the anterior end of the fenestra hypophyseos (Fig. 4). In the younger stages the cerebral hemispheres lie immediately dorsal to the orbitosphenoid region, but in the adult they are quite far posterior to it, and the olfactory tract surrounded on each side by a gelatinous mass extends above it. The anterior end of the jugular vein enters the cranium through the orbital foramen and proceeds posteriorly along the dorsal surface of that part of the orbitosphenoid which forms the wall of the cavum cranii.

The earlier descriptions were confusing because of the absence of this bone in some of the lower teleosts, especially since it is absent in the perch, Cuvier's type of fish cranium. The present identity of the bone with the *ala orbitales* of mammalian anatomy is derived from the work of Hallmann (1837). He recognized Cuvier's error in naming the petrosal, the *ala magna* and hence confusing the homologies of the more anterior parts. Since the bone next in front of the petrosal in mammals was the *ala magna* of the sphenoid, and since this bone in the carp had relations corresponding to it, the name was applied. The bone in front of this was then compared to the '*ala parva*' and found to correspond, hence it was named. Agassiz (1842) and Stannius (1853) did not adopt this homology, but named the bone the *os ethmoideum*. The

name, orbitosphenoid, given to the bone by Owen (1848), is in general use at the present time.

In many of the lower teleosts, where a large interorbital septum is developed, the orbitosphenoid is lacking. Among these are Scomber, the Loricati (Allis, Gutberlet); Perca (Cuvier, Hallmann); Osteoglossum, Gonorhynchus, Chanos (Ridewood, 1904); Gasterosteus (Swinnerton, 1902); and others not referred to here.

In *Amia* (Sagemehl, 1884) the orbitosphenoid is paired and lies on the cartilage above the anterior margin of the optic foramen, separated from the bones above and in front by cartilage. In *Arapaima* (Ridewood, 1904), it is paired, but unlike *Amia*, these ossifications extend from the frontals to the parasphenoid. In those species with a medium sized interorbital septum as *Salmo* (Parker, 1872); *Alepocephalus* (Gegenbaur, 1878), and some of the Cyprinidae (Sagemehl, 1891), the orbitosphenoid is unpaired and Y-shaped, the arms of the Y extending up in the walls of the cranium and the basal part down into the orbital septum. It always lies above the anterior margin of the optic fenestra and usually the basal piece ossifies as far ventrally as the trabecula communis. In the Characinidae the bone has various gradations in structure from the U-shape corresponding to that of *Amiurus*, to the Y-shaped Salmonoid type. Of all the forms studied I think that the orbitosphenoid as found in *Homolopterus* of the Characinidae is the closest in orbitosphenoid relations to *Amiurus*. There is the same strongly ossified midventral piece, and the same general relations to the surrounding bones and to the optic nerve. The orbital foramen is also present between the orbitosphenoid and the ectethmoid of each side and considerable cartilage remains within the bone, a strip of it persisting between the frontals and upper ends of the inner surface of the bone.

Vrolik (1873) maintained that, because the orbitosphenoid is an inconstant bone and because it could be developed from either the membrane of the interorbital septum or from cartilage, that it could not be homologized throughout the different groups. The fact of its relation to the nerve foramina, its gradation in development in the lower forms all aid in proving that it was a paired bone in the ancestral teleosts, and that it was originally developed from cartilage. Cartilaginous cells are present in the interorbital septum of those forms in which the septum is decidedly primitive, a circumstance which may be taken to indicate that there has been a shortening of the ontogeny of the septum in the higher forms where the septum ossifies directly.

*The parasphenoid* (Figs. 6, 7), is a long, flat, unpaired bone extending on the ventral surface of the cranium from the supraethmoid to the anterior end of the basioccipital. Its anterior interdigitation with the supraethmoid is hidden by the vomer. The median anterior end of the parasphenoid is kept from contact with the ethmoid cartilage or internasal septum by the supra-

ethmoid (Fig. 7). The posterior spicules of the supraethmoid are inserted in grooves on the ventral surface of the parasphenoid. The anterior lateral margins of the bone, fitting tightly against the cartilage of the ethmoid plate, are separated from the ectethmoids by a narrow interval. Posterior to the supraethmoid, the orbitosphenoid is developed between the parasphenoid and the chondrocranium. In this region the parasphenoid is limited to the ventral surface of the orbitosphenoid; the arcus palatini muscles are inserted in a groove on each side of the former. The projection ventral to this groove ends posteriorly in a little knob ventral to the trigemino-facial foramen (Figs. 6, 20). At the posterior end of the orbitosphenoid the parasphenoid expands laterally to form the posterior margin of the optic foramen, interdigitating dorsally with the alisphenoid. Behind the alisphenoid the parasphenoid interdigitates with the prootic and with it forms the ventral posterior margin of the trigemino-facialis foramen. The posterior end of the parasphenoid is inserted in grooves on the ventral surface of the basioccipital.

Behind the orbitosphenoid, the parasphenoid is excluded from the floor of the cavum cranii by the suprasphenoid. In the younger stage the suprasphenoid develops on the cerebral surface of the parasphenoid and is firmly connected with it, even in the 32 mm. stage (Fig. 32). There are spaces in the floor of the cranium close behind the orbitosphenoid between the para- and suprasphenoid in the adult which show where the cartilage has been resorbed (Fig. 7), but traces of cartilage are present also. Sagemehl, in his study of the Characinidae and the Cyprinidae, did not recognize a suprasphenoid element ankylosed to the cerebral part of the parasphenoid, but described the floor of the cavum as formed by the parasphenoid. It is evident that, had he studied the development of this region, he would have identified two elements in the composition of his parasphenoid. He states that in the Cyprinidae the parasphenoid forms the posterior end of the interorbital septum when such is present. In all of the other teleosts, as *Salmo*, with a medium sized interorbital septum, the part of the septum posterior to the optic foramina and anterior to the hypophysis is formed by a Y or T-shaped suprasphenoid (basisphenoid of the usual terminology). The parasphenoid always forms the support of the basal part of the Y. In *Amiurus* there is no basal part to the Y, consequently the arms lie directly upon the cerebral surface of the parasphenoid and it is only by the study of the development of this region that the two elements are recognizable. Even in the adult the two elements are recognizable to a certain degree in the median section of the cranium (Fig. 7), where the posterior end of the orbitosphenoid and the anterior end of the prootic are enclosed by the parasphenoid externally and the suprasphenoid internally.

In those fishes which have a well developed eye-muscle canal—*Salmo*, *Scomber*, and the *Loricati*—the parasphenoid is separated from the prootic bones by the lumen of the canal, the floor and part of the side walls of which are formed by the parasphenoid. In *Amiurus* the parasphenoid is fused to the

ventral surface of the prootics (Fig. 7). The wings which extend dorso-laterally between the orbitosphenoid and the prootic, are characteristic of the teleostean parasphenoid. In some forms they lie behind the fifth nerve and in others in front of it, which Swinnerton regards as of importance in establishing the morphology of the bone. The ridge for the insertion of the arcus palatini muscles is characteristic of the ventral surface of the parasphenoid. There are usually two of these ridges as in *Amiurus*, but in *Scomber* (Allis, 1903) they have fused into a single ridge along the middle line of the bone.

Before Huxley, the parasphenoid was regarded as the homologue of the mammalian basisphenoid and was called the 'sphenoidae basilare.' Huxley (1864) recognized the peculiar relation of this bone to the ventral surface of the cranium and denied this homology because it extended beneath the anterior bones of the cranium and posteriorly beneath the basioccipital, and was easily detached from the chondrocranium. He limited the distribution of the parasphenoid to the branchiate vertebrates and this idea was prevalent until Sutton (1884) maintained that the bone was present in the higher groups and that it was the representative of the vomer of the mammals. Its great development in the fishes and in the Amphibia is due to the weak base of the chondrocranium. With the highly ossified condition of the sphenoidal cartilages of the Mammalia the bone was no longer needed as a support of the cranium and so it became a part of the septum of the nasal passages.

The development of the parasphenoid from membrane below the anterior basicranial fenestra has been known for a long time in many groups and, as noted above (page 43), the development in *Amiurus* is typical. In some of the lower teleosts, among which is *Osteoglossum* (Ridewood, 1904), the parasphenoid bears teeth, but it is not known whether they are primarily an integral part of the developing bone or have fused with it later.

*The suprasphenoid.* This bone in *Amiurus* is in a very unspecialized condition as compared with those teleosts which have an interorbital septum. It lies cerebral to the parasphenoid and is firmly fused to it (Fig. 7). It occupies the floor of the cavum cranii between the optic and trigeminal nerves; anteriorly it overlaps the orbitosphenoid, posteriorly the prootic. Laterally, between the foramina for these nerves, it interdigitates with the alisphenoid. As stated above, it is developed from membranous connective tissue between the trabeculae in the fenestra hypophyseos (Fig. 32). It has all the characters common to the suprasphenoid bone of the other teleosts, except the eye muscle relations. The homologies of this bone have been discussed earlier in the paper, as the terminology used is based principally upon its developmental relations.

*The alisphenoids.* These are a pair of bones, one on each side of the cranium between the optic and trigemino-facial foramina (Figs. 7, 20). Their ventral ends are separated externally from each other by the parasphenoid, and inter-

nally by the suprasphenoid. The former is usually sutured to the alisphenoid between the ventro-posterior margin of the optic foramen and the antero-ventro-margin of the trigemino-facial foramen. An anterior process of the alisphenoid extends ventrally as the anterior margin of the optic foramen, descending in the orbital wall as far as the orbitosphenoid. This interdigitation between the alisphenoid and orbitosphenoids continues dorso-posteriorly to the anterior end of that part of the frontal which overlaps the dorsal margin of the alisphenoid. The latter extends higher up in the cranial wall than does the more anteriorly situated orbitosphenoid. Above the trigemino-facial foramen the alisphenoid interdigitates with the anterior margin of the ventral part of the sphenotic, the line of interdigitation continuing forward between the sphenotic and the frontal. The sphenotic projects broadly above this part of the alisphenoid and a concavity is formed between them by the lateral projection of the alisphenoid. The ligament of the dilator operculi muscle is inserted on the roughened face of the alisphenoid in this concavity. The very anterior margin of the hyomandibula articulates with the posterior edge of the alisphenoid below the ligament insertion.

The ophthalmic branch of the trigeminus issues from the cranium through a foramen in the wall of the alisphenoid just postero-dorsal to the optic foramen, and extends anteriorly along a ledge above the latter. This foramen is the outer end of a short canal which proceeds posteriorly within the alisphenoid and has its cerebral opening near the posterior ventral margin of the internal surface of the bone (Fig. 7). The ophthalmic branch of the facial passes anteriorly through a more dorsal canal. Although its cerebral opening is just dorsal to the cerebral opening of the ophthalmic branch of the trigeminus, the external opening of the canal is farther forward than the external opening of the latter, and lies just posterior to the point where alisphenoid, frontal and orbitosphenoid meet. The manner in which these nerves are included within the bone is first seen in the 32 mm. stage (Fig. 4). Up to that time the nerves, after leaving the cartilage, extend free across the orbit, but with subsequent development they are gradually enclosed by the ossification of the connective tissue around them in connexion with the alisphenoid cartilage, so that eventually the adult condition is reached. The ventral end of the bone is formed by the ossification of the original membranous wall between the optic and trigeminal nerves (Fig. 32). This method of development of the alisphenoid from cartilage and membrane has been noted in *Salmo* (Schleip 1903).

The cerebral surface of the alisphenoid bone is smooth and presents the same relations to the surrounding bones as the external except at its ventral margin, where it is overlapped by the dorsal projection of the suprasphenoid (Fig. 7). The anterior margin of the alisphenoid, where it meets the orbitosphenoid, has not entirely replaced the underlying cartilage, which still shows through the thin surface lamella. There is probably some cartilage yet remaining between the dorsal cap of the alisphenoid and the ventral surface of the

frontal. The inner ends of the canals for the ophthalmic branches of the fifth and seventh nerves have been discussed above. McMurrich noted both of these canal openings, but only one nerve. He stated (1884b) that the upper opening "opens into the interior of the bone like other similar foramina which perhaps, have a nutritive function." In reality this foramen is the posterior end of a canal for the passage of the ophthalmicus branch of the facial nerve and not for a blood vessel. He also says that the ventral margin of the alisphenoid bone articulates with the basisphenoid (suprasphenoid, auct.) alone and does not touch the parasphenoid, but from a study of sections through this region, I think that para- and suprasphenoids are fused along the ventral margin of the bone and that the external surface is the parasphenoid and the internal, the suprasphenoid. I cannot find any point where alisphenoid meets the prootic as he maintains, but since this is common in most of the teleosts, there is a possibility that such was the condition in the specimens he studied although it is present in none of mine.

An historical review of the various names which this bone has borne since the earliest descriptions of it by Meckel, Arendt, Cuvier, and others, is given by Owen (1848), Vrolik (1873), and Starks (1901). Since the orbitosphenoid was lacking in the perch, which Cuvier used as his type, he caused confusion in the literature by regarding the alisphenoid as the homologue of the ala orbitalis and the prootic as the ala magna. Hallman (1837), as noted above, recognized the true homology of the bone and called it the ala magna, because of its relation to the first branch of the trigeminus. Huxley's work on the homologies of the basal part of the cranium helped to define the criteria for the identification of the bone as it is known today. Owen, at the same time, ignored Huxley's conclusions and regarded the bone as the orbitosphenoid because of its relation to the optic nerve. At present all ichthyologists agree that this bone has approximately the same relations to the surrounding bones as has been described for *Amiurus* and the term alisphenoid is in common use. Yet, as stated above, some do not regard it as the homologue of the greater wing of the mammals.

In fishes with a well developed interorbital septum, the orbitosphenoid is wanting and the alisphenoid is correspondingly reduced in size. Scomber (Allis, 1903), the Loricati (Allis, 1910), and *Alepocephalus* (Gegenbaur, 1878), are good examples of this limitation in the development of the bone. In spite of its size in these forms, the alisphenoid usually encloses a small foramen for the ophthalmic branch of the fifth nerve, just posterior to the optic. In *Megalops* (Ridewood, 1904) the alisphenoids meet in the roof of the cranium. In *Gasterosteus* (Swinnerton, 1902) the alisphenoids are lacking, their place being taken by dorsal spiculae of the parasphenoid.

The Cyprinidae (Sagemehl, 1891) approach nearest to the type of alisphenoid found in *Amiurus*, and in *Catostomus* there is the same anterior projection of the bone. Stannius (1853) recognized this high development of the ali-

sphenoid as typical of the cyprinoids and siluroids, basing his observations on *Silurus glanis* and *Cyprinus carpio*. Vrolik's figure of *Silurus glanis* also shows a well developed alisphenoid.

The developmental relations of the bone have been discussed above, but it may be added that the roughened surfaces for the attachment of muscles and ligaments of the adult is developed from the muscle fascia and connective tissue surrounding the perichondrial lamella of the alisphenoid cartilage.

*The sphenotics.* Next to the frontals, these are the most conspicuous paired bones on the dorsal surface of the cranium (Fig. 10). Each is subquadrangular in shape and has long interdigitating margins, projecting into the surrounding bones. Anteriorly, each interdigitates with the posterior margin of the frontal, the line between these two bones being continuous posteriorly with the sphenotic-supraoccipital interdigitation. The posterior margin of the dorsal surface of the bone extends in between the squamoso-pterotic and the posterior end of the supra-occipital, almost touching the transverse crest of the latter. The anterior lateral margin of the sphenotic is raised slightly, so that a dilatator groove is formed along the latero-dorsal surface, for the insertion of part of the dilatator operculi muscle and ligament. The surface of the bone is without ridges and the lateral line canal ossification has sunken below the surface and is invisible from above. The only foramina on the dorsal surface of the bone are several for the passage of twigs of the ramus oticus of the facial.

The lateral surface of the bone is grooved for articulation with the hyomandibula (Fig. 20). This surface is ossified, but the face of the hyomandibula which articulates with it, is still cartilage. The beginning of the ossification in this region has been shown earlier (Figs. 19, 33). The articular facet is continuous posteriorly with a similar groove on the lateral face of the squamoso-pterotic, and below it the two bones are separated from each other by a narrow strip of cartilage, which extends ventrally as far as the prootic bone (Fig. 20). The line of interdigitation between sphenotic and prootic extends antero-ventrally from the ventral end of this piece of cartilage and continues as far anteriorly as the dorso-posterior margin of the trigemino-facial foramen. From this point as far forward as the mid-dorsal margin of the foramen the sphenotic alone forms the margin. Here it comes in contact with the posterior end of the alisphenoid and the suture between them extends dorso-ventrally as far as the region where the sphenotic meets the frontal. Viewed from above the ventro-external extent of the sphenotic is not very great.

The internal surface of the bone forms an almost square area in the cranial wall, from the dorsal margin of the trigemino-facial foramen to the supraoccipital (Fig. 7). Anteriorly it is in contact with the alisphenoid in the margin of the same foramen and above this with the frontal. The interdigitation with the frontal continues posteriorly as the line between sphenotic and supraoccipital. Posteriorly the sphenotic meets the prootic and the continuation of this suture to the supraoccipital is restricted by a small square of cartilage. A



shallow recess about in the center of the cerebral surface of the sphenotic contains the cerebral end of a canal through which the ramus oticus facialis passes and which emerges by several foramina on the dorsal surface as already mentioned. The anterior end of the recess for the anterior semicircular canal lies within the bone, but the canal itself does not extend to the end of the recess. The internal surface of the recess, noted above as filled with trabeculae (Figs. 33, 36), has now entirely ossified so that this part of the sphenotic bone is solid. Cartilage between the inner and outer lamellae of the bone has not been entirely replaced, traces of it occurring between the pterotic and the sphenotic. The large cartilaginous roof present in the 32 mm. stage between the supraoccipital and the medial dorsal edge of the sphenotic (Fig. 3) has been covered by perichondrial ossification continuous with the latter. The lateral line ossification has become an integral part of the bone, although restricted to a very small area (Fig. 11). There are no sense organs within the lateral line canal in the sphenotic nor are there any tubules leading to the exterior.

From Cuvier (1826) to Parker (1872), the sphenotic was regarded as the homologue of the postfrontal of the reptiles, and so named. Parker first called it the sphenotic and described it in *Salmo* as an ectosteal ossification of the otic capsule above the ampulla of the anterior semicircular canal, thus grouping it with the other otic bones described by Huxley (1864). Up to that time the criterion for the homology of this bone was based upon morphological rather than ontogenetical relations. Vrolik (1872) devotes a short paragraph to the names which this bone has borne in the older literature, but calls it the postfrontal and describes it in the teleosts as a 'perichondrostische ossifikation,' the equivalent of a dermal bone of the present paper. In *Amia* (Bridge, 1877; Sagemehl, 1884) the bone was called the postfrontal, until Allis (1898) revised the nomenclature of the problematical bones of this animal, and called it the postorbital ossification. The use of this term was unfortunate because he had already applied the name postorbital to a bone of the infraorbital series as the homologue of the reptilian postorbital. The name postfrontal was given to the superior dorsal bone of the infraorbital chain and from his definition of it, I have followed him in naming its homologue in *Amiurus*. In *Scomber* (Allis, 1903), he uses the same confusing terms, postorbital bone and postorbital ossification for postorbital and sphenotic respectively, justifying his terminology, on the basis, that they should not convey any relationship to the bones of the higher groups. The term sphenotic as used by Parker is more expressive of the developmental relations of this bone than the terminology of Allis and, as this bone is strictly a piscine and avian ossification, no confusion will arise through its use. Allis (1910) evidently has changed his views and has called the homologous bone of the Loricati, the sphenotic.

Ridewood (1904) maintains that the term postfrontal should be retained because it describes the uppermost surface of the bone, the lateral line element. According to Allis (1898) the postfrontal never fuses with an underlying peri-

chondrial ossification and hence this part of the sphenotic is not comparable to the true postfrontal. He does not attempt to explain to what bone this dermal derivative may be compared. In *Amiurus*, as in many other teleosts, the perichondrial ossification on the chondrocranium is fused with a dorsally lying lateral canal ossification (Figs. 19, 33). McMurrich also noticed this in his work on *Amiurus*. If the postfrontal of *Amiurus* is to be regarded as the superior infraorbital bone, then this lateral line canal ossification, above the sphenotic, must be an element which has no homologue in the higher groups and is developed for the protection of the canal alone, eventually sinking in and becoming intimately connected with the perichondrial ossification. That it takes only a minor part in the formation of the broad roof of the bone can be seen by the way in which the major part of the bone is developed medial to it on the surface of the otic capsule.

The homologies of the remaining parts of the bone in the Teleostomes are easy to trace. The lateral face is usually grooved for articulation with the hyomandibula and is related in *Amiurus* to the anterior and posteriorly situated bones. In most Teleostomes the sphenotic does not have the ventral extent found in *Amiurus*, nor does it occupy as much of the dorsal surface of the cranium. In *Scomber* (Allis, 1903) and the *Loricati* (Allis, 1910), the relations of the ramus oticus facialis are comparable to the condition in *Amiurus*.

There is a great deal of cartilage within the bone and sometimes, as in *Salmo*, there is no internal ossification. The relation of the bone to the recess for the anterior semicircular canal is a constant feature, although in most fishes the canal extends only part way into it.

In some of the Cyprinidae the lateral part of the dorsal surface of the bone is grooved for the insertion of the dilator operculi ligament and muscles as in *Amiurus*. In other teleosts this fossa lies more upon the posterior margin of the frontal than upon the sphenotic. It may be said however, that the sphenotic usually forms a part of the dilator fossa.

*The prootics.* These bones form the floor and most of the lateral walls of the cavum cranii, posterior to the suprasphenoid and the foramina for the passage of the seventh nerves. As noted above (Figs. 4, 26), they develop around the anterior parachordals and the ventral part of the otic capsules. They are fused with each other in the median line of the cranial floor, below and posterior to the hypophysis. A large amount of the original cartilage remains in both the lateral and ventral parts of the bone, for the most part encased in a perichondrial osseous lamella and continuous with the cartilage of the surrounding bones (Fig. 7). That part of the bone which forms the posterior margin of the trigemino-facial foramen is exceedingly thin and transparent. In tracing the development it was noted that the cartilage which originally formed the posterior margin of the foramen in the 10 mm. stage did not keep pace with the growth of the cartilage of the surrounding parts, so that in the 32 mm. stage,

a thin lamella of bone formed the margin, as if the cartilaginous connexion between the parachordal and otic capsule had been stretched, until only the ossified perichondrium remained between them (Fig. 4). The other thin part of the bone lies near its posterior margin, just dorso-posterior to its suture with the basioccipital (Fig. 20). This part was formed from the outer lamella alone, as is stated in the discussion of the 32 mm. stage, and was solid cartilage in the 10 mm. stage.

The external surface of the bone is smooth, except for a shallow depression near the dorsal margin where the adductor hyomandibularis is inserted (Fig. 20). The bone is almost square in outline and has anterior, dorsal, and ventral edges serrated, where they overlap the other bones. The posterior margin is straight and is separated from the exoccipital by a thin strip of cartilage. Antero-dorsally it interdigitates with the sphenotic below the hyomandibular facet, but takes no part in the formation of the latter. Dorso-posteriorly this line of interdigitation continues between the prootic and the anterior end of the pterotic. Ventro-anteriorly it is overlapped by the parasphenoid and behind by the basioccipital. No foramina are present in the body of the bone for the passage of nerves or blood vessels as these all leave by the trigemino-facial foramen.

The internal surface of the bone is not as regular in outline nor does it present the same smoothness as the outer (Fig. 7). As remarked above, the bones of the two sides are fused in the middle line and their anterior edges are overlapped by the posterior margin of the suprasphenoid bone which extends from the ventral margin of one trigemino-facial foramen across the floor of the cranium to the other. There is a shallow depression in the floor of the cranium just behind this contact with the suprasphenoid, the sella turcica, for the hypophysis. The floor of the sella is very thin, but immediately posterior to it there is a massive ridge, the dorsum sellae, which is continuous posteriorly with the bulk of the basioccipital bone. This is not completely ossified, but considerable cartilage, continuous with that within the basioccipital, remains between the inner and outer lamellae.

The median section shows the relations of the prootics to the parasphenoid and basioccipital in this posterior region (Fig. 7). The recessus sacculorum project anteriorly into the posterior ends of the prootics and medial to them the transverse suture between the inner lamella of the prootics and the basioccipital is visible. In the 32 mm. stage (Fig. 27) a thin horizontal lamella from the median cartilage extends laterally above the anterior end of each recessus to the ventral edge of the otic capsule, but no lamella was yet formed on the floor of the recessus. In the adult, this basal lamella is present and, together with a lamella of the basioccipital, extends ventrally into the recess. The prootic lamella forms both floor and side walls of the recessus and is fused with the ventral face of the horizontal lamella, but the basioccipital lamella meets a descending lamella of the exoccipital half way up in the lateral wall. Thus in

the dorsal part of the lateral wall of each recessus sacculi the posterior margin of the prootic is sutured to the exoccipital. This suture continues laterally in the labyrinth recess as far as the base of the lateral septum semicircularis. The bulk of this septum persists as cartilage and separates the lateral margin of the prootic from the exoccipital. A lamella of the prootic extends up on the anterior face of the cartilage and its dorsal end is separated from the posterior ventral margin of pterotic part of the squamoso-pterotic and the inner lamella of the supraoccipital by cartilage. Anteriorly, in the floor of the lateral recess, the prootic meets the pterotic and the line between them extends anteriorly as far as the outer end of the anterior septum (Fig. 7). This septum is also partly cartilage, and the prootic lamella embraces its ventral surface and is confluent with the inner surface of the wall of the anterior recess, formed by a vertical projection from the floor of the prootic. In the younger stage this wall was cartilage and showed the beginnings of perichondrial ossification on both its cerebral and labyrinthine surfaces. The cartilage at the cerebral end of the septum anterior separates the prootic lamella from the supraoccipital.

I have not been able to find the eye-muscle canal which McMurrich (1884b) described as occurring between the prootic, parasphenoid and basioccipital. These bones are very tightly pressed together in this region and there is no space between them.

Cuvier (1826) first described this bone in the fishes as the homologue of the human *ala magna*. About the same time Meckel (1824) recognized it as the homologue of the petrosal because of its relation to the labyrinth and the facial nerve. His ideas were further elaborated by Hallmann (1837), who revised the nomenclature of the bones in this region, but retained this name. Stannius (1853) called it the *ala temporalis* because of its general similarity to the temporalis of the mammals. As is well known Huxley (1864) homologized this bone in *Esox* with one of the three ossification centers of the petrosal part of the temporalis of man and called it the prootic. Some of the modern authors have, nevertheless, retained the term petrosal, although on comparison with the petrosal of mammals it can be compared only to the part defined by Huxley.

The prootic is one of the constant bones of the piscine cranium and usually has the same general relations to the anterior semicircular canal and the facial nerve. In those teleosts which have an eye-muscle canal (*Salmo*, *Scomber*, the *Loricati*, etc.) the facialis issues through the bone, separate from the trigeminus. In groups in which the eye-muscle canal is not developed, as in *Amiurus*, the facialis issues through a notch in the anterior edge of the prootic. In most forms, whether an eye-muscle canal be present or not, the median ventral ends of the bones of the two sides are fused in the floor of the cranium. The eye-muscle canal usually lies ventral to the median ends of these bones, which form its roof. The parasphenoid in such cases forms the floor and part of the side walls of the canal. The presence of a large amount of cartilage within the bone has been remarked in *Scomber* and the *Loricati* (Allis), and in some of the

Cyprinidae (Sagemehl, 1891), and in *Salmo* (Parker, 1872). It is not remarkable to find it where the chondrocranium is persistent to a very great degree in other parts, but in *Amiurus*, where there is a great deal of ossification, it is significant of the primitiveness of this region.

In some of the Clupeoid fishes (Ridewood, 1904), the basicapsular fenestra, which occurs in larval *Salmo* (Parker, 1872; Gaupp, 1906), is a constant feature in the adult between the prootic, parasphenoid and basioccipital bones.

In *Perca* (Cuvier, 1826; Hallman, 1837), *Carpio* (Cuvier, Hallman, Stan-  
nius, 1853; Sagemehl, 1891), *Pleuronectes* (Cole and Johnson, 1901), the prootic forms the lower part of the hyomandibular facet. In *Salmo*, *Scomber*, the *Loricati*, and many other forms, there are separate foramina in the bone for the passage of carotid arteries, jugular vein and the hyomandibularis ramus of the facialis. In *Amiurus*, some, but not all of the blood vessels communicate with the internal parts of the cranium through the large trigemino-facial foramen. In *Scomber*, the external surface is grooved as in *Amiurus* for the insertion of the adductor hyomandibularis; the same thing is possibly true for most fishes, but has not been stated in the descriptions.

*The squamoso-pterotics.* In the 32 mm. stage both the squamosal and the pterotic were in their initial stages and the perichondrial and dermal elements which make up the adult compound bone were just beginning to fuse in the wall of the otic capsule above the lateral semicircular canal (Fig. 31). In places, the cartilage had been resorbed and the inner and outer lamellae were connected by osseous trabeculae. The lateral line canal, which in the older stage, is invisible from above, at that time formed a slight ridge on the dorsal surface of the cartilage and was fused to the underlying perichondrial ossification. In the adult, the outer surfaces of the bone, both lateral and dorsal, are made up almost entirely of ossified membrane and muscle fascia (Figs. 6, 10, 20). This led some authors who had not carefully studied the development, to conclude that the whole bone was entirely a dermal ossification, and hence comparable to the squamosal part of the temporalis of man.

The lateral line canal ossification of the adult becomes an integral part of the dorsal surface of the bone and connects postero-laterally with the superior end of the opercular-mandibular canal and the main lateral canal of the body (Fig. 11). The former passes into the latero-posterior corner of the bone from the dorsal one of two subtemporal lateral line ossicles, the margin of which is fastened to the squamosal part of the bone by ligamentous tissue. Before leaving the squamosal that part of the canal which is to pass into the body issues to the surface, and runs posteriorly on it for a short distance before passing into the post-temporal. There are two sense organs in the lateral line canal within the squamoso-pterotic.

The dorsal surface of the squamosal part of the bone is subtriangular in outline and with serrated edges overlaps the surrounding bones. Anteriorly it

articulates with the sphenotic, medially with the supraoccipital, and posteriorly with the epiotic (Fig. 10).

There is no temporal fossa, but there is a space between the squamosal and pterotic parts, which may be a remnant of it. The latero-posterior end of the bone projects broadly and on its surface is the groove for the lateral line canal before it enters the post-temporal. Connective tissue fibres extend from its margin to the margin of the operculum, holding the latter in place.

The ventral surface of the bone is grooved and ridged for the insertion of the fibres and ligaments of the adductor operculi muscle (Fig. 6). This face of the bone is sculptured more than is the dorsal; it is formed by the ossification of the fascia and connective tissue external to the original perichondrial ossification. The latter ossification shows in two places on this surface—anteriorly on the margin below the hyomandibular articular surface, and posteriorly on the postero-ventral margin of the bone. In both of these places the bone is a very thin lamella separated from the bone nearest it by cartilage; the cartilage is continuous within the lamella of both of the bones. Anteriorly it is separated from the sphenotic and posteriorly from the exoccipital by cartilage. Between these two bones the outer lamella interdigitates with a similar lamella of the prootic, and close examination of this part shows considerable cartilage yet remaining beneath these layers. Postero-dorsally it interdigitates with the epiotic.

The dorso-lateral margin of the bone is grooved for articulation with the hyomandibular and is entirely ossified in all parts. As noted above, this facet for the hyomandibular continues anteriorly on to the sphenotic. There are several foramina in the ventral surface of the bone which lead into its interior, but do not communicate in any way with the cavum cranii. Several blood vessels and some loose connective tissue fill this space and the region immediately external to it.

Internally, the pterotic lamella is limited to the lining of the recess for the lateral semicircular canal and the anterior wall of the posterior (Fig. 7). In the floor of the recess it interdigitates with the prootic lamella, but is separated from the internal lamellae of the other bones—supraoccipital and epiotic—by the cartilage of the lateral septum and the roof of the recess. In the very lateral extremity of the recess, the cartilage has been resorbed, a process beginning in the 32 mm. stage (Fig. 31). For the most part, however, inner and outer perichondrial lamellae are separated by persisting cartilage.

The squamosal part of the bone is the only part found in *Amia* (Sagemehl, 1884), and it is distinctly separated from the chondrocranium by a space filled with connective tissue and the anterior ends of the body musculature. There is also a lateral line element fusing with the squamosal in *Amia* just as in *Amiurus*, and the canal, upon leaving the squamosal, pursues the same course. *Amiurus* repeats the condition which Sagemehl described for most of the Characinae and Cyprinidae, where a squamosal unites with a pterotic element.

This author has stated that in some of the forms with a thick cutis, the lateral line canal ossification never fuses with the squamosal element and hence both are independent ossifications. The internal relations of the pterotic lamella are the same as in *Amiurus*, and cartilage persists to a great extent within it and the surrounding bones. In those forms where the sphenotic is small (*Scomber*, *Salmo*, the *Loricati*, etc.) and limited to the anterior edge of the otic capsule, the squamosal element of the bone extends anteriorly and articulates with the frontal. The lateral line canal, which in *Amiurus* passes first through the sphenotic and thence into the squamosal, in these forms passes directly from the frontal into the squamosal. The squamosal element of the bone is usually limited medially by the parietal, but in *Amiurus* it has fused with the supraoccipital. There is always a ridge or a groove on the ventral surface of the squamosal part for the support of the shoulder girdle, and another groove on the lateral face, for articulation with the hyomandibula.

Cuvier called this bone the 'os mastoideum,' homologizing it with the mastoid portion of the temporal bone of human anatomy. Hallman (1837) recognized it as the homologue of the squamosal element of the temporal, and, regarding the bone from adult conditions, this was a logical conclusion, as he did not study its development. Both of these authors used the cranium of *Perca* and Hallman also made a detailed study of the cranium of *Cyprinus*. Huxley (*Esox*) called the bone the squamosal and did not recognize its relation to the chondrocranium. Parker (1872) says that he tried to point out to Huxley the fact that in *Salmo* the bone developed in connexion with the wall of the lateral semicircular canal and hence was comparable to another otic ossification center. Huxley would not entirely grant his views, but in his book remarked that in the opinion of Parker, the bone under consideration was a true otic bone. Thus it remained for Parker (1872) to designate it as the pterotic in *Salmo*. According to this view it was developed entirely as a chondrocranial bone and did not have the elements which were recognized later by Gaupp and Schleich. They called it the dermo- and autosquamosal according to the suggestion of Van Wijhe (1882) for the naming of the parts of mixed bones. Sagemehl found both elements in the *Characinidae* and the *Cyprinidae*, but called the whole the squamosal. Allis calls this bone by differing names in his papers, and in his work on the *Loricati* (1910) designates the bone as the pterotic followed by squamosal in parenthesis, giving an erroneous synonymy to the first term.

*The epiotics.* These are a pair of bones on the latero-posterior dorsal angles each of the cranium. Each lies between the squamoso-pterotic, the supraoccipital and the exoccipital of its side (Figs. 9, 10). Each is pyramidal with the apex on the posterior surface of the cranium and has three faces, the first on the dorsal surface of the cranium, the second on the posterior surface below the apex, and the third on the latero-ventral surface (Fig. 6). The dorso-anterior surface of the bone bears a strong vertical crest, along the anterior face of which some opercular-mandibular muscle fibres have their insertion. The median

prong of the post-temporal bone is firmly fastened by ligament to the posterior surface. A ligament of the trapezius muscle is attached to the crest below the post-temporal. The crest itself continues medially on the supraoccipital.

At first sight this part of the bone appears as an isolated element, because the squamoso-pterotic bone extends in beneath the crest, and apparently separates this part of the bone from the more posterior portion. Closer inspection shows that the crested part of the bone and the more posterior part are a continuum, although the latter is rugose and concave just behind the crest, giving the impression that the crested part of the bone is a separate piece. The posterior part of the bone slopes ventrally to form part of the posterior surface of the cranium (Fig. 9). Medially it is separated from the supraoccipital by a strip of cartilage which continues around the ventral margin of the bone, there separating it from the exoccipital. Above this, on the lateral surface of the cranium it interdigitates with the pterotic part of the squamoso-pterotic. This portion of the epiotic is thin and concave ventrally for the insertion of fibres of the adductor operculi muscle. It does not develop from the perichondrium of the otic capsule, but by ossification of connective tissue around the ends of the muscle fascia.

The posterior surface of the bone is corrugated for the insertion of the ends of the trapezius muscle fibres. Thus the external surface of the epiotic bone is covered with a superficial ossification developed from muscle fascia, which covers most of the outer perichondrial lamella.

The internal surface of the bone forms the posterior and dorsal walls of the recess for the posterior semicircular canal. Most of the wall is completely ossified and the cartilage has been resorbed except along the margins of the bone. In the earlier stages this part of the otic capsule had an inner lamella which was connected across the walls of the recess by osseous trabeculae (Fig. 38), and which now forms the solid central part of the posterior wall of the recess.

Although it has been definitely demonstrated by Huxley, Parker, Schleip and Gaupp, that the epiotic bone of the teleosts is a distinct otic ossification developed from the posterior dorsal part of the otic capsule wall, the Cuvierian name 'occipitale externum' is still prevalent in the literature. Sagemehl (1884) modified the term and called it the 'exoccipitale' in his work on *Amia*, the Characinidae and the Cyprinidae. Allis followed him and in all except his most recent papers has named it according to Sagemehl, although this introduces confusion with the true exoccipitals.

In all of the teleosts this bone lies at the posterior dorsal angle of the cranium as in *Amiurus*, and bears more or less of a crest for articulation with the post-temporal part of the shoulder girdle. Sometimes the epiotic is limited more to the dorsal surface of the posterior region of the otic capsule, but usually a part of it extends ventrally as the hinder wall of the posterior semicircular canal. Its homologies are evident throughout the teleosts and even in most ganoids it is a well developed ossification.



*The supraoccipital.* This is a large unpaired bone which forms the median cranial roof behind the frontals. Its anterior margin is divided into halves by the posterior end of the posterior fontanelle, on the margins of which it meets the frontals (Fig. 10). The portions of the bone along the fontanelle are raised above the level of the surrounding bones and form a ridge which is continuous anteriorly with a similar ridge on the frontals and posteriorly with the medial surface of the occipital spine. Muscles of the opercular and mandibular apparatus have their insertion along the sides of these ridges. At the base of the ridge the supraoccipital interdigitates with both the sphenotic and squamoso-pterotic.

Near the posterior margin of the dorsal surface, a crest, continuous with that of the epiotic, meets the longitudinal ridge at right angles and a cavity is formed by their intersection (Fig. 10). The crest curves postero-dorsally and forms the lateral margin of the dorsal surface of the spina occipitis, a triangular osseous splint which projects posteriorly from the dorsal surface of the cranium. Between the crests of the two sides the dorsal surface of the spine has the shape of a trough, the floor of which is irregularly excavated for the insertion of muscle fibres. The ventral edge of the spine is connected to the posterior dorsal surface of the supraoccipital proper by a thin osseous sheet, which, as noted above (Fig. 29), is developed by the ossification of the connective tissue between the anterior muscles.

Behind the crest the main portion of the supraoccipital bone descends on the posterior surface of the cranium as far as the exoccipital bones (Fig. 9). Laterally, there is an interdigitation between the upper medial margin of the epiotic and the supraoccipital, which continues anteriorly into the crest. The ventrolateral margin of the supraoccipital is separated from the epiotic by a strip of cartilage, continuous ventrally with that between the epiotic and exoccipital. The ventral margin of the supraoccipital interdigitates with the dorsal margin of the exoccipital in the wall of the foramen magnum, where there is also a strip of cartilage between them. The supraoccipital forms a very small part of the wall of the foramen. Just above the foramen the supraoccipital is embraced by the anterior ventral surface of the anterior spine of the compound vertebra, which, as stated in the account of the development of this region, is the neurapophysis of the third neural arch, the first two neural arches being modified as parts of the Weberian apparatus. The whole external surface of the posterior face of the bone is rugose and bears ridges for the attachment of muscle fibres.

The internal surface of the bone is very smooth and for the most part is only a superficial lamella on the cartilage around the dorsal ends of the septa semicircularia (Fig. 7). Anteriorly, on each side, it interdigitates with the frontal and laterally with the sphenotic; each side is separated from the posterior end of the sphenotic by a small area of cartilage at the dorsal end of the septum semicircularis anterior. The bone extends over the cartilage between

the anterior and lateral septa, but does not meet the pterotic lamella which lines the lateral recess. It forms an osseous sheath on the anterior face of the posterior septum and encloses the fenestra for the passage of the posterior membranous canal. Below this fenestra it meets the exoccipital. The inner end of the canal for the passage of the ramus lateralis accessorius of the facial nerve and the jugular vein lies in a recess in the bone above the fenestra. In median section this bone shows itself to be well ossified and thick, especially in that region which forms the margin of the posterior fontanelle. Laterally, the inner and outer lamellae are separated by cartilage.

This is one of the best developed bones of the adult teleost cranium and usually has a long posteriorly projecting spine attached to its dorsal surface. Cuvier recognized it in *Perca* and stated that, while it might possibly be regarded as the interparietal, he preferred to describe it as the homologue of the reptilian supraoccipital. Hallman (1837) figures it in *Cyprinus* and *Perca*, but gives no detailed description. Parker (1872) was the first one to describe the development of the bone in detail in the teleosts, as arising from perichondrial lamellae on the occipital arch and synotic tectum, between the parietals, and touching the frontals anteriorly. In *Salmo* the margins of the bone are rounded and there is not the spiculate serrate edge found in *Amiurus*. Sagemehl (1885) described the bone in the *Characinidae* briefly, and commented upon the extent of the occipital spine, with the remark that from its relations to the muscle, there was evidence that it had been developed from the fascia between them and has secondarily fused with the main part of the bone developed on the occipital arch. In his discussion of the bone in the *Cyprinidae*, he states an hypothesis for the development of the bone from the ganoid condition, where it is wanting, by assuming that the occipital arch in the teleosts, upon which the supraoccipital bone developed, arose from the assimilation of the first vertebrae in a ganoid ancestor of the teleosts, and that there is no evidence for regarding the bone as a derivative of the dermal plates in this region of *Polypterus*, *Acipenser*, *Lepidosteus* and *Amia*. Loomis (1900) has shown in the fossil ganoids of Kansas, that the supraoccipital is absent, although present in the fossil teleosts. Zittel (1884, 1893) and Woodward (1898) have described this same condition in the fossil Teleostomes. But in a previous discussion, it was concluded that the vertebra at the anterior end of the vertebral column were not serially homologous in the different groups and that segments can be intercalated and excalated. So instead of regarding the supraoccipital as the homologue of a neural process of the ganoids, it must be assumed to be a new part which is intercalated as a new formation in the teleosts, but at what time this intercalation took place there are no fossil records. The homologue of the supraoccipital plates of *Polypterus* is the spina occipitis. This has been developed from connective tissue above the occipital arch and is fused to the underlying supraoccipital ossification. In the *Stegocephali* (Fritsch, 1883), there are a pair of supraoccipital plates corresponding to those

of *Polypterus*, and going yet higher in the vertebrate series we find that two pairs of connective tissue ossifications have been described attached to the dorso-anterior margin of the cartilaginous supraoccipital in man, the interparietals and the preinterparietals (Ficalbi, 1890; Ranke, 1899). The latter are inconstant, but the former may be the bones which correspond to the spina occipitis of the teleosts and the supraoccipital plates of the *Stegocephalans*.

McMurrich (1884b) states that in *Amiurus* the dorsal surface of the spina occipitis is perforated with foramina for the passage of tubules connected with the 'mucous' canal system; an error since the canal system has no branches in the posterior part of the cranium outside of the squamosal part of the squamoso-pterotic. Further, he says that the 'ascending branch' of the first spinal nerve (my hypoglossus) issues from the cranium through the foramen for the ramus lateralis accessorius facialis. As I have not been able to find a dorsal branch of this nerve in either the younger or the older specimens, I cannot agree with him

*The exoccipitals.* The floor and side walls of the foramen magnum are formed by the paired exoccipital bones (Fig. 9). Nearly the whole margin of each bone is smooth except for a few interdigitating spicules on the epiotic and supraoccipital edges. It is separated anteriorly from the pterotic part of the squamoso-pterotic and the posterior margin of the prootic bone by a strip of cartilage which continues ventro-posteriorly between it and the antero-dorsal margin of the basioccipital. On the posterior surface of the cranium it is separated from the epiotic by the cartilage, but interdigitates with the ventral margin of the supraoccipital as far as the wall of the foramen magnum where cartilage is present between the bones.

The anterior ventral surface of the bone is pierced by two foramina, a small anterior one for the glossopharyngeal and a larger one immediately posterior for the vagus (Fig. 20). The ossification separating them is a very delicate osseous spicule and was originally cartilage. Just behind the vagus foramen there is a sharp, upwardly curved prong, to which the transcapular bone is attached. This latter bone has developed from the ossification of a ligament between the shoulder girdle and the cranium (Fig. 37). Ventral to the articulation of the transcapular with this bone, the surface of the exoccipital is rugose for the attachment of the fibres of the shoulder girdle muscles. On the posterior surface of the cranium the bone is concave medial to the base of prong, and at the bottom of this concavity there is a minute foramen for the passage of the hypoglossus nerve. A flange of the bone projects posteriorly behind this foramen at right angles to the posterior surface of the cranium, forming part of the lateral wall of the foramen magnum. This part of the bone develops from the ossification of the membranous sheet, present in the younger stages, posterior to the hypoglossus, and fuses with the ventral end of the occipital arch. The posterior ventral margin of the bone is fused with the dorsal surface of the thickened basioccipital.

Within the cranium, the anterior margin of the bone interdigitates with the prootic as far laterally as the base of the lateral septum semicircularis, and medially as far as the roof of the recessus sacculi (Fig. 7). Behind the lateral septum semicircularis, the exoccipital lamella extends laterally over the floor of the recess for the posterior semicircular canal, and part way up its posterior wall. It is separated by cartilage from the more lateral and dorsal pterotic and epiotic lamellae. The inner ends of the foramina for the glossopharyngeal and vagus nerves lie in this part of the bone. Medial to the posterior recess, a part of the bone extends out dorsally and, with the supraoccipital, forms a wall between the recess and the cavum cranii. At the base of this wall a horizontal process extends medially above the recessus sacculi and meets a similar process from the other side to form the roof of the sinus impar. The ventral surface of this process meets a splint from the basioccipital, which forms the side wall of the cavum sinus imparis and the roof of the recessus sacculi of that side. The lateral wall of the recessus sacculi is formed by exoccipital and basioccipital lamellae.

The foramen for the hypoglossus nerve lies posterior to and above the lateral end of the horizontal process. The latter forms the ventral margin of the foramen magnum, and between it and the dorsal surface of the basioccipital the sinus impar leaves the cranium to divide into the atria sinus imparis. The posterior ventral end of the exoccipital is fused with the basioccipital.

The exoccipital bone is one of the most constant bones throughout the vertebrate series. It is fairly well developed in all higher groups of ganoids, although considerable cartilage remains between the inner and outer lamellae. As in *Amiurus*, it forms the floor and side walls of the foramen magnum and there is usually a gap of cartilage in the dorsal margin of the foramen where in *Amiurus* the supraoccipital lies. In some teleosts—*Salmo*, *Citharinus*, and *Catostomus*—the cartilage persists in this region.

The anterior margin of the bone usually encloses the ninth and tenth nerves, either in a single foramen or an anterior and a posterior opening, and ossification usually starts in the cartilage around these foramina. The intercalated nerves are secondarily enclosed in the posterior part of the bone, as in *Amiurus*. In the Cyprinidae (Sagemehl, 1891), this foramen is larger and is divided into two parts, one for the ventral and the other for the dorsal root of the nerve. The dorsal foramen is very large in *Catostomus*, *Cyprinus*, and *Cobitis*, and, above the nerve, is filled with lymphatic tissue continuous with the contents of the saccus paravertebralis of the Weberian apparatus. Sagemehl claims that the larger has arisen by the fenestration of a single original foramen such as occurs in *Amiurus*.

Ostariophysian teleosts have a median horizontal process on each exoccipital, which, with its fellow of the opposite side, forms the cranial floor above the sinus impar and the recessus sacculorum. Actual contact of the exoccipital with the surrounding bones is not usually the case, because cartilage per-

sists between them. In this same group of fishes there is usually a ligament extending from the basioccipital to the shoulder girdle (Sagemehl, 1885), which he says is the homologue of the transcapular process of *Amiurus*.

The synonymy of this bone has been given by Owen (1848), Vrolik (1873), and Starks (1901). To their list of synonyms may be added the name given to this bone by Gaupp (1906), *pleurooccipitale*. Of all the names, *exoccipital*, suggested by Owen, is the briefest, and most comprehensive of the relations of the bone; *pleurooccipitale* has no excuse.

*The basioccipital.* This is the most posterior bone on the ventral surface of the cranium and is fused on its ventral face to the anterior centrum of the compound vertebra of the spinal column. The bulk of the bone lies in this immediate region and thins out anteriorly on the ventral and lateral surfaces of the cranium (Fig. 6). Its ventro-anterior margin is overlapped by spicules of the parasphenoid and its dorsal anterior surface by the posterior margin of the suprasphenoid and the prootic (Fig. 7). The dorso-lateral margin of the anterior end of the bone interdigitates externally with the extreme posterior ventral margin of the prootic (Fig. 20). Behind this interdigitation the basioccipital is separated from the antero-ventral margin of the exoccipital by cartilage until the two exoccipitals fuse posteriorly. Below this fusion the posterior face of the basioccipital is circular and deeply concave (Fig. 9). The edges of the concave anterior face of the centrum of the first vertebra is fused with the periphery of this face of the basioccipital and in the space enclosed between the faces is filled with gelatinous notochordal tissue. A small space in the ventral surface of the basioccipital just anterior to its fusion with this centrum remains unossified and is filled with cartilage, the remnant of the hypochordal cartilage of the 32 mm. stage (Fig. 38).

The internal surface of the bone is hollowed out for the reception of the sacculi. It forms the median crest between the recessus sacculorum and part of their floor and side walls. The dorsal surface of the crest is concave, forming the floor and walls of the cavum sinus impar. In the side wall of each recessus the internal basioccipital lamella meets the descending lamella of the exoccipital of that side. In the 32 mm. stage this had already completely ossified and so in the adult there is no cartilage left in the walls of the recessus except between the margins of the bones. Considerable cartilage yet remains in the basal plate between the posterior end of the prootic and the basioccipital (Fig. 7). There is no trace of the intercranial notochord so prominent in the younger stages.

The transcapular bone has part of its attachment to the lateroventral surface of the basioccipital (Fig. 9).

The basioccipital of the teleosts is very constant in its morphological relations. As in *Amiurus*, its posterior face is concave where attached to the centrum of the first vertebra and the gelatinous mass is nearly always present between them. In the Ostariophysi the sacculi penetrate more deeply into

the substance of the basioccipital than they do in other teleost groups, but the sacculi always have a relation to the dorsal surface of the bone. The interdigitation of basioccipital with parasphenoid, and articulations with prootic and exoccipital, are common characters. The processes on the bone for articulation with the transscapular process are peculiar to the Siluridae. The pharyngeal processes of the Characinidae and Cyprinidae, extending from the ventral surface of the basioccipital to the wall of the swim-bladder, are not found in other teleosts. Allis (1910) mentions a groove on the dorsal surface of the basioccipital in the Loricati, which he claims as the homologue of the *cavum sinus imparis* of the Ostariophysi. The basioccipital throughout the teleosts is usually excluded from participation in the formation of the foramen magnum by the union of the posterior ends of the exoccipitals above it or by the presence of the *sinus impar*.

The bulk of the bone is developed from the posterior parachordalia and the ossification of the intercranial notochord. In some of the Cyprinidae considerable cartilage remains in those parts of the bone which form the walls and floor of the recessus sacculorum. In all of the teleosts, the notochord disappears in that part of the basioccipital anterior to the vertebral articular surface. In the forms with an eye-muscle canal, the basioccipital forms its posterior floor.

*The premaxillaries* are a pair of bones forming the anterior end of the upper jaw and are closely fused with each other in the mid-ventral line of the cranium. They have no ascending process, such as occurs in *Salmo*, *Scomber*, *Alepocephalus* and other teleosts, but are closely fused to the ventral surface of the supraethmoid bone. They curve posteriorly on each side to form the osseous floor of the nasal fossae and are attached by ligament to the palatine and maxillary bones dorso-posteriorly. The ventral surface of each bone is covered with teeth, which, as mentioned in the younger stage are only secondarily connected with it (Fig. 15).

*The maxillaries.* Each maxillary bone (Fig. 15) lies latero-posterior to the premaxillary, embedded in the connective tissue forming the lateral margins of the upper lips. Each is toothless and serves as a support for the elongate, laterally extending, maxillary barbel. This lateral position of the maxillary is common among the teleosts and occurs in *Amia* also. In *Salmo*, the bone is continuous posteriorly with the premaxillary and bears a series of teeth on its ventral surface. In *Scomber* it lies partly internal to the premaxillary and has an articular surface for it. In the Loricati the bone has a long posterior extent and overlaps the mandible. In none of these forms is it as small as in *Amiurus* where it has a slender styliform shape and is held in position partly by connective tissue. It is in actual contact with the palatine bone, articulating with it by means of a small ball and socket joint, the latter lying on the palatine.

*The palatines.* These bones retain the same shape and relations as in the younger stages, although now much larger in size (Fig. 15). Ossification has proceeded in all parts and there is only a core of cartilage left. Each palatine is a slender dumb-bell shaped ossification lateral to and below the ectethmoid process with which it has articulated from its earliest stage. The anterior ventral end is grooved for the articulation with the maxillary, and the pre-maxillary is attached to these two bones by tough connective tissue. As earlier, so now, the palatine has no actual contact with the pterygoquadrate ossification. In *Salmo* the bone is continuous posteriorly with the bones of the pterygoid arch and bears teeth on its ventral surface. In the Characinidae, the palatine bone has varying sizes and shapes, but it is developed on cartilage continuous posteriorly with the cartilage within the pterygoid bones. In *Erythrinus*, the maxillary articulates with the palatine in the same manner as in *Amiurus*, but the palatine does not extend as far forward. In *Scomber* (Allis, 1903), the palatine is fused with the anterior bone of the pterygoid series and bears teeth.

*The ectopterygoid.* This bone develops by the ossification of a sheet of connective tissue ventral to the palatine and connected with it by connective tissue (Fig. 15). The posterior margin interdigitates with the anterior margin of the large metapterygoid. McMurrich (1884b) described this bone as 'number four' and stated that it could not be homologized with a pterygoid bone because it was developed from membrane. Schleip (1903) found that it developed from membrane in *Salmo* and that it is separated from the pterygoid cartilage by connective tissue and yet maintains that it is the homologue of the ectopterygoid of other teleosts. The bone is very small, quadrate in outline, with delicate sculptured radiating lines. In *Salmo* it is longer and thinner than in *Amiurus* and has more of the character of the corresponding bone in *Amia* (Van Wijhe, 1882), the Characinidae and the Cyprinidae. There is no entopterygoid in *Amiurus*.

*The metapterygoid.* This large bone is developed around the pterygoid part of the pterygoquadrate cartilage. It is quadrangular in outline and interdigitates anteriorly with the ectopterygoid, posteriorly with the hyomandibular and ventrally with the quadrate (Fig. 15). No cartilage persists in any of the visible parts of the bone. Medially it is attached to the lateral surface of the cranium by a sheet of muscular and ligamentous tissue. A mesopterygoid occurs in most teleosts between the meta- and ectopterygoids, but in *Amiurus* the two interdigitate. In *Scomber* a small strip of cartilage intervenes between the metapterygoid and the quadrate and there is a space between the former and the elongate hyomandibular bone. In *Salmo* (Parker, 1873) the bone is not nearly as great in extent, occupies a position entirely dorsal to the quadrate and is separated from the latter, as in *Scomber*, by cartilage. It does not interdigitate with, but overlaps the hyomandibular.

In *Megalops* (Ridewood, 1904), a large ectopterygoid hinders its anterior extent and it overlaps the hyomandibular posteriorly. In *Pleuronectes* (Cole and Johnson, 1901), it is smaller than in *Amiurus* and lies posterior and dorsal to the quadrate. The small metapterygoid of the Characinidae is separated from the ectopterygoid and quadrate by cartilage and there is also a large foramen between it and the latter.

*The quadrate.* This bone is situated at the ventro-anterior end of the hyomandibular suspensorial apparatus (Fig. 15). It is grooved on its inferior face for articulation with the mandible. It is rather small, and firmly fused to the surrounding bones, although there is a small area between it and the hyomandibular, where the underlying persisting cartilage shows between the bones. Its posterior face interdigitates with the preopercular bone. Mc-Murrich (1884) states that the cartilage mentioned as occurring between the bones is the symplectic and that in perfectly dried skulls there is a space between the hyomandibular and the quadrate due to the absence of cartilage.

*The hyomandibular.* This large bone connects the quadrate with the cranium. It is immovably fused with the latter and if one moves, both must. A process of the bone projects from the anterior edge to the lateral surface of the alisphenoid which is hollowed out for its reception. Posterior and dorsal to this point of contact the hyomandibular articulates with the side of the cranium in a groove which has been described in connexion with the sphenotic and squamoso-pterotic bones. There are several ridges on the lateral surface of the bone along which the adductor muscles are attached (Fig. 15). Just above its interdigitation with the preopercular is a foramen for the passage of the ramus hyomandibularis facialis. The knob for the articulation of the operculum has ossified and is overlapped by the ventral surface of this bone, which is hollowed out as a socket for movement on the knob.

In *Salmo* (Parker, 1873), the hyomandibular does not have the anterior and ventral extent that it has in *Amiurus* and it is isolated from the surrounding bones by cartilage. Parker does not figure the foramen for the hyomandibularis nerve, but from Gaupp's figure (1906) of the foramen in the younger stage of *Salmo*, it is evident that the nerve passes farther forward than in *Amiurus*. In the Albulidae and Mormyridae, and other lower teleosts, the hyomandibular does not have so great an anterior, posterior, or ventral extent as in *Amiurus*, and usually a small symplectic element comes between it and the quadrate. The preopercular does not articulate with the hyomandibular as closely as in *Amiurus*. In all of the teleosts the hyomandibular has a knob on its posterior edge for the articulation of the operculum; in some of the Characinidae cartilage persists at this point.

*The dentary.* The teeth which are borne on the lower jaw are attached to the medial dorsal surface of this bone, from the symphysis as far back as the dentary-articular interdigitation. The bone retains the shape and relations



which it had in the younger stages. It tapers anteriorly where it meets the fellow of the opposite side and is deeper posteriorly (Fig. 15). The inner surface of the bone is hollow for the reception of the anterior end of Meckel's cartilage. The ventro-anterior surface is perforated by a series of six pores for the passage of tubules of the enclosed mandibular lateral line canal (Fig. 11). The canal issues from the mandible through the more posterior pore and enters the connective tissue surrounding the quadrate and thence passes into the preopercular. I agree with McMurrich that the dentary is a mixed bone and is the result in part of the ossification of a portion of Meckel's cartilage. The developmental stages show that the bone is at first arises entirely from the connective tissue membrane around the cartilage fused with a lateral line ossification; later part of Meckel's cartilage ossifies and fuses with it (Fig. 24).

*The articulare.* This is a triangular bone at the posterior end of the mandible and is grooved on its posterior face for articulation with the quadrate (Fig. 15). It does not contain a lateral line element. The internal dorsal surface is flat and gives attachment to the muscles which move the lower jaw. Considerable cartilage persists between the outer and inner lamellae. The bone bears no teeth and interdigitates anteriorly with the dentary, which also extends posteriorly in a groove on its ventral surface.

*The preopercular.* The mandibular-opercular lateral line canal enters the bone from the connective tissue surrounding the posterior ventral end of the quadrate (Figs. 11, 15). The bone is fused solidly to the quadrate ventrally, and to the hyomandibular dorsally. A small process projects down behind the quadrate and the opercular canal passes into this part.

The posterior edge is ridged and projects above the more posterior lying operculum. The dorsal end of the bone extends for a short distance behind the hyomandibular. There is a small foramen in the middle part of the bone for passage of a branch of the hyomandibularis facialis as it descends after passing through the hyomandibular.

*The subtemporals.* These are two small bones lying dorsal to the preopercular and above the posterior margin of the hyomandibular (Figs. 11, 15). They contain the dorsal end of the opercular lateral line canal which passes through them into the squamosal. They are very thin and the canal in passing through them, lies in a groove rather than in a tube, the ventral and lateral walls of which are thicker than the very thin roof. Only one such bone, having the same relations to the lateral line canal and the squamosal is found in this region of *Salmo*. Parker (1872) called it the supratemporal, but the supratemporal of the stegocephalans always lies medial to the squamosal so that this bone could not be its homologue. Ridewood (1904) suggests the term adopted here and says that the real supratemporal of *Salmo*, between the back of the squamosal and the post-temporal, was overlooked by Parker, but it is really

larger than the subtemporal. Sagemehl (1885) states that these bones are present in many of the Siluroids.

*The opercular apparatus.* This consists of three bones; a large dorsal operculum and two smaller ventral bones, the inter- and suboperculum, (Fig. 15). The operculum spreads out posteriorly in a wide arch and articulates anteriorly with the hyomandibular knob. It is heavily sculptured on its external surface, tapers ventrally, and at its inferior apex the short quadrangular interoperculum is attached by ligamentous tissue and interpolated between it and the posterior end of the articulare. The suboperculum is smaller and lies medial to the interoperculum.

## SUMMARY

1. The chondrocranium of *Amiurus* is platybasic.

2. In the chondrocranium of the 10 mm. *Amiurus* there is no internasal septum; the epiphysial bar is the only part of the chondrocranium dorsal to the brain; it divides the opening in the roof of the primitive skull into an anterior and a posterior fontanelle.

3. The olfactory foramen lies in a sagittal plane and is very large in comparison with the olfactory tract. A solum nasi is present. The ectethmoid process, a short transverse projection between the nasal fossa and the orbit, is perforated by the ophthalmicus superficialis trigemini. An orbital foramen is present posterior to the ectethmoid process.

4. Trabecular and alisphenoid cartilages form the margins of a large fenestra in the lateral wall of the cranium for the passage of the optic, oculomotor, trigeminal, abducens, and facialis nerves. The fenestra is closed by membrane at the 10 mm. stage, except where the nerves pass.

5. The alisphenoid cartilage is the homologue of the ala magna of the mammalian chondrocranium.

6. The cavum labyrinthii opens directly into the cavum cranii; there are three septa semicircularia; no basicapsular fenestra is present; the glossopharyngeal and vagus nerves issue from the cranium between the otic capsule and the parachordal plate. The otic capsules are fused posteriorly with the occipital arch; a synotic tectum is lacking in the 10 mm. *Amiurus*. The hyomandibular articular surface lies external to the lateral semicircular canal.

7. The parachordal cartilages lie lateral to the intercranial notochord, are fused anteriorly with the trabeculae, dorso-laterally with the otic capsules, and posteriorly with the occipital arch. The notochord forms the axis of the posterior part of the solid parachordal plate. The sacculi lie in recesses on the dorsal surface of the parachordal plate on each side of the notochord.

8. The ventral ends of the occipital arch are fused with the parachordals posterior to the vagus foramen; the posterior end of the arch is inserted into the anterior end of the third neural arch. The hypoglossus nerve has dorsal and ventral roots united within the vertebral canal and a single lateralis ramus issuing between the occipital arch and the anterior process of the scaphium. The nerves posterior to the hypoglossus have the rami characteristic of true spinal nerves and alternate with the neural arches. Two pairs of myotomes are present lateral to the occipital arch, but their innervation by the nerves in

this immediate region could not be clearly made out. The two pairs of myotomes following these are innervated by the second and third pairs of post-vagal nerves.

9. The beginnings of the premaxillary and maxillary bones are present in the 8 mm. *Amiurus*.

10. The palatine cartilage is independent of the pterygoquadrate, and the latter is fused to the hyomandibular.

11. Ossification is present in the skull of the 32 mm. *Amiurus*. The large dorsal fontanelles of the 10 mm. stage are limited to mere slits by the frontal and supraoccipital ossifications; the epiphysial cartilage persists, but lies relatively further posterior; a rudimentary tegmen cranii and synotic tectum are present; a massive cartilaginous internasal septum divides the olfactory tracts; the olfactory foramina lie in a transverse plane.

12. The supraethmoid bone has both membrane and perichondrial ossifications entering into its composition. The perichondrial ectethmoid ossification is fused with a connective tissue ossification on the lateral margin of the ectethmoid process. The foramen orbito-nasale lies relatively more posterior than in the 10 mm. stage; perichondrial ossifications appear on the margin of the orbital foramen.

13. The fenestra hypophyseos is closed by the orbitosphenoid, parasphenoid, suprasphenoid, and prootic ossifications.

14. The intercranial extent of the notochord is apparently less than in the 10 mm. stage, but this is due to the greater relative growth of the cartilaginous parts surrounding it.

15. The suprasphenoid bone is developed from membrane in the floor of the cranium and is not the homologue of the basisphenoid of the mammalian cranium, but is a bone peculiar to the teleosts.

16. A squamosal ossification, developed from membrane, fuses with the pterotic ossification; as the latter has no homologue in the mammalian petrosal, the resulting bone of the adult cannot be a temporalis, but must be regarded as a squamoso-pterotic.

17. The spina occipitis of the supraoccipital bone arises from membrane and is the homologue of the supraoccipital plates of the *Stegocephali* and probably of the interparietal element of the mammalian cranium.

18. The skull of the adult *Amiurus* is well ossified, although considerable cartilage persists in the ethmoid and otic regions. The adult cranium resembles, in many points, the crania of some of the *Characinidae* and *Cyprinidae*.

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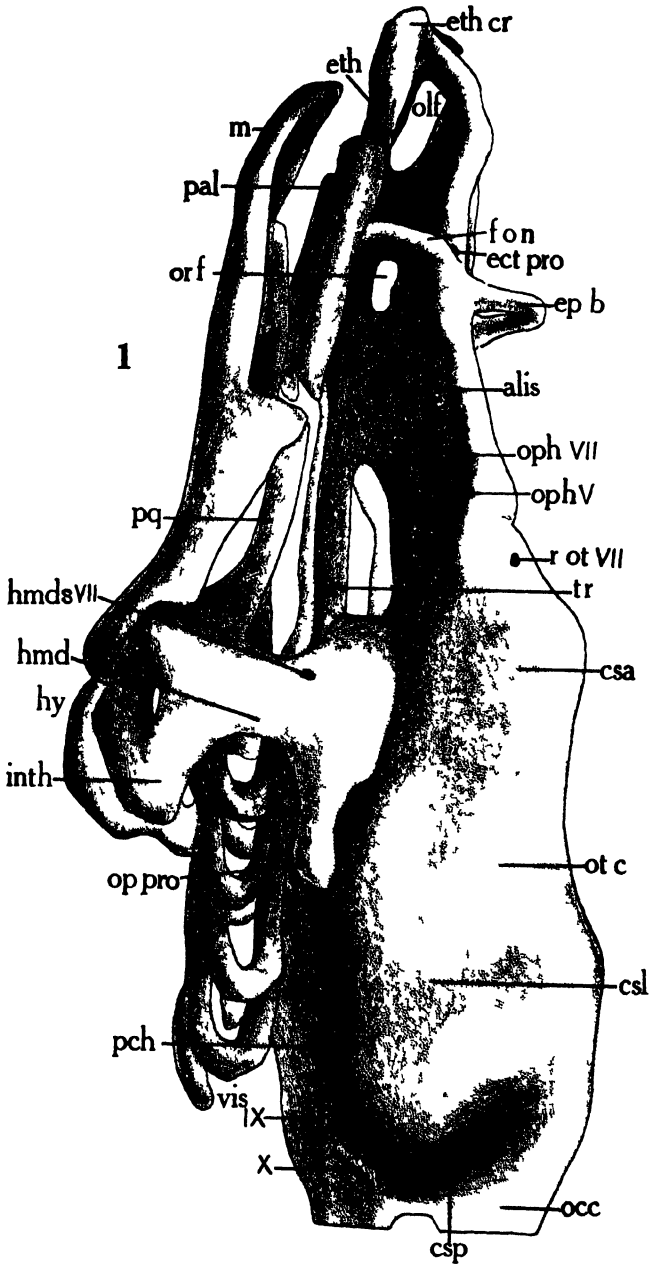
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## PLATE I

## EXPLANATION OF PLATE

Fig. 1.—Lateral view of model of chondrocranium of *Amiurus* 10 mm. long.

<i>alis</i>	alisphenoid bone	<i>oph V</i>	foramen for ophthalmicus superficialis trigemini
<i>csa</i>	anterior semicircular canal	<i>oph VII</i>	foramen for ophthalmicus superficialis facialis
<i>csl</i>	lateral semicircular canal	<i>op pro</i>	opercular process
<i>csp</i>	posterior semicircular canal	<i>or f</i>	orbital foramen
<i>ect pro</i>	ectethmoid process	<i>ot c</i>	otic capsule
<i>ep b</i>	epiphysial bar	<i>pal</i>	palatine
<i>eth</i>	ethmoid plate	<i>pch</i>	parachordal
<i>eth cr</i>	ethmoid cornu *	<i>pq</i>	pterygoquadrate cartilage
<i>f o n</i>	foramen orbito-nasale	<i>r ot VII</i>	ramus oticus facialis foramen
<i>hmd</i>	hyomandibular	<i>tr</i>	trabecula cranii
<i>hmds VII</i>	hyomandibularis branch of VII	<i>vis</i>	visceral arches
<i>hy</i>	hyoid arch	<i>IX</i>	glossopharyngeal foramen
<i>inth</i>	interhyal	<i>X</i>	vagus foramen
<i>m</i>	Meckel's cartilage		
<i>occ</i>	occipital arch		
<i>olf</i>	olfactory foramen		





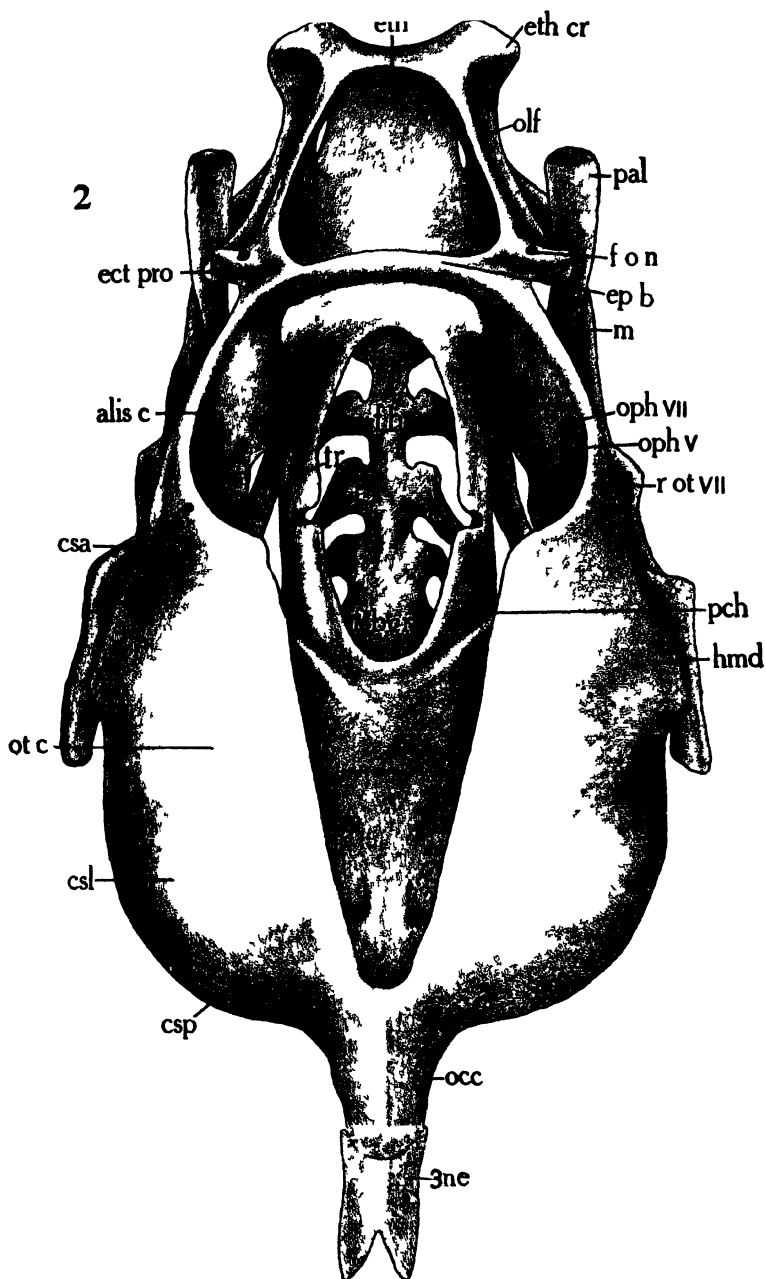
**PLATE II**



## EXPLANATION OF PLATE

Fig. 2.—Dorsal view of chondrocranium of *Amiurus* 10 mm. long.

<i>alis c</i>	alisphenoid bone	<i>m</i>	Meckel's cartilage
<i>ca</i>	foramen for internal carotid artery	<i>occ</i>	occipital arch
<i>csa</i>	anterior semicircular canal	<i>olf</i>	olfactory foramen
<i>csl</i>	lateral semicircular canal	<i>oph V</i>	foramen for ophthalmicus superficialis trigemini
<i>csp</i>	posterior semicircular canal	<i>oph VII</i>	foramen for ophthalmicus superficialis facialis
<i>ect pro</i>	ectethmoid process	<i>ot c</i>	otic capsule
<i>ep b</i>	epiphysial bar	<i>pal</i>	palatine
<i>eth</i>	ethmoid plate	<i>pch</i>	parachordal
<i>eth cr</i>	ethmoid cornu	<i>r ot VII</i>	ramus oticus facialis foramen
<i>f bcr</i>	fenestra basicranii anteriorius	<i>tr</i>	trabecula cranii
<i>f h</i>	fenestra hypophyseos	<i>3ne</i>	third neural arch
<i>f o n</i>	foramen orbito-nasale		
<i>hmd</i>	hyomandibula		





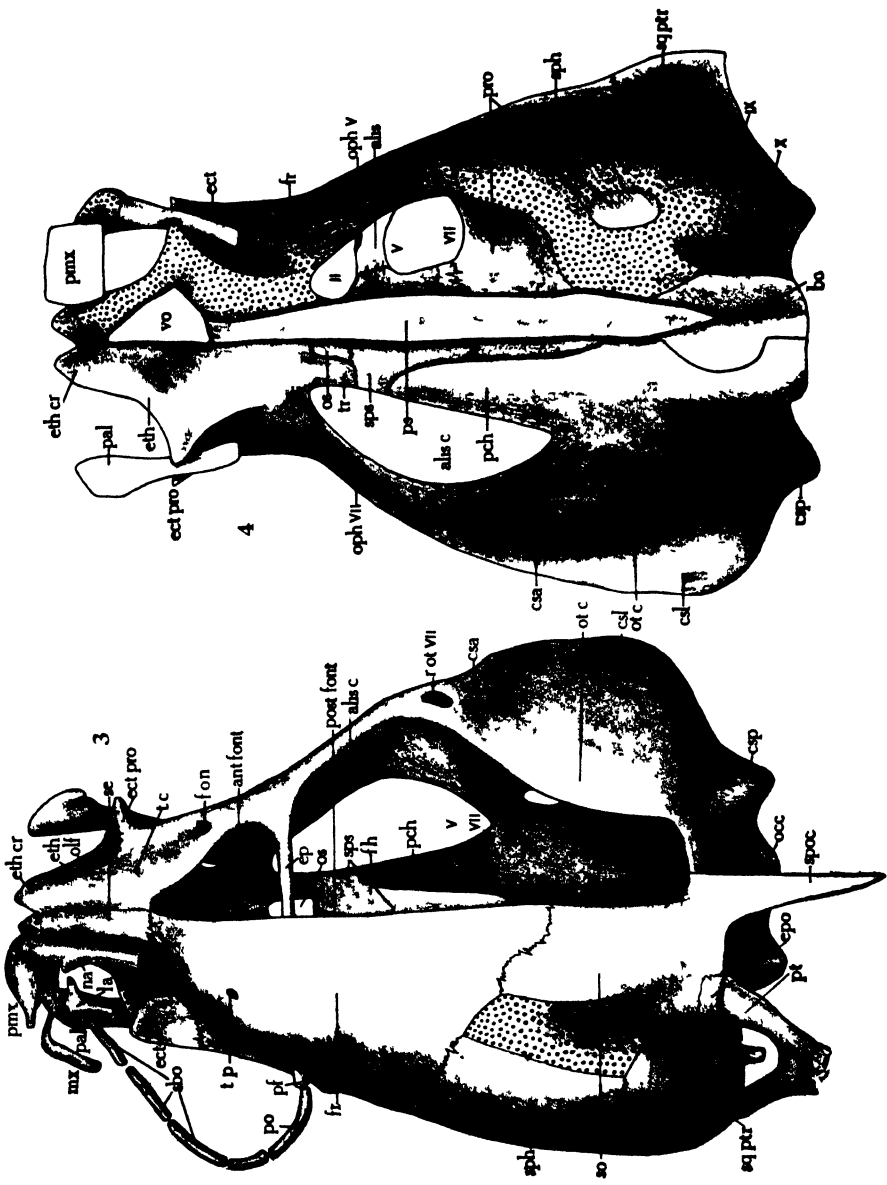
## PLATE III

## EXPLANATION OF PLATE

Fig. 3.—Model of chondrocranium of 32 mm. *Amiurus*, dorsal view. On the right side only cartilage parts are shown, on the left the bones as well, cartilage being stippled to contrast with the bones.

Fig. 4.—Same, ventral view, cartilage only on left side, cartilage and bone on right of drawing.

<i>alis</i>	alisphenoid bone	<i>ot c</i>	otic capsule
<i>alis c</i>	alisphenoid cartilage	<i>pal</i>	palatine
<i>ant font</i>	anterior fontanelle	<i>pch</i>	parachordal
<i>bo</i>	basioccipital	<i>pf</i>	postfrontal
<i>csa</i>	anterior semicircular canal	<i>pmx</i>	premaxillary
<i>csi</i>	lateral semicircular canal	<i>po</i>	postorbital
<i>csp</i>	posterior semicircular canal	<i>post font</i>	posterior fontanelle
<i>ect</i>	ectethmoid	<i>pro</i>	prootic
<i>ect pro</i>	ectethmoid process	<i>ps</i>	parasphenoid
<i>ep</i>	epiphysial	<i>pt</i>	post-temporal
<i>epo</i>	epiotic	<i>r ot VII</i>	ramus oticus facialis foramen
<i>eth</i>	ethmoid plate	<i>sbo</i>	suborbitals
<i>eth cr</i>	ethmoid cornu	<i>se</i>	supraethmoid
<i>f h</i>	fenestra hypophyseos	<i>so</i>	supra occipital
<i>f o n</i>	foramen orbito-nasale	<i>sph</i>	sphenotic
<i>fr</i>	frontal	<i>spoc</i>	spina occipitis
<i>la</i>	lacrimal	<i>sps</i>	supraorbital canal
<i>mx</i>	maxillary	<i>sq ptr</i>	squamoso-pterotic
<i>na</i>	nasal	<i>tc</i>	tegmen cranii
<i>occ</i>	occipital arch	<i>tp</i>	tubule pore of lateral line canal
<i>olf</i>	olfactory foramen	<i>tr</i>	trabecula cranii
<i>oph V</i>	foramen for ophthalmicus super- facialis trigemini	<i>vo</i>	vomer
<i>oph VII</i>	foramen for ophthalmicus super- facialis facialis	<i>II</i>	optic foramen
<i>os</i>	orbitosphenoid	<i>V-VII</i>	foramen trigemino-facialis
		<i>IX</i>	glossopharyngeal foramen
		<i>X</i>	vagus foramen





## PLATE IV



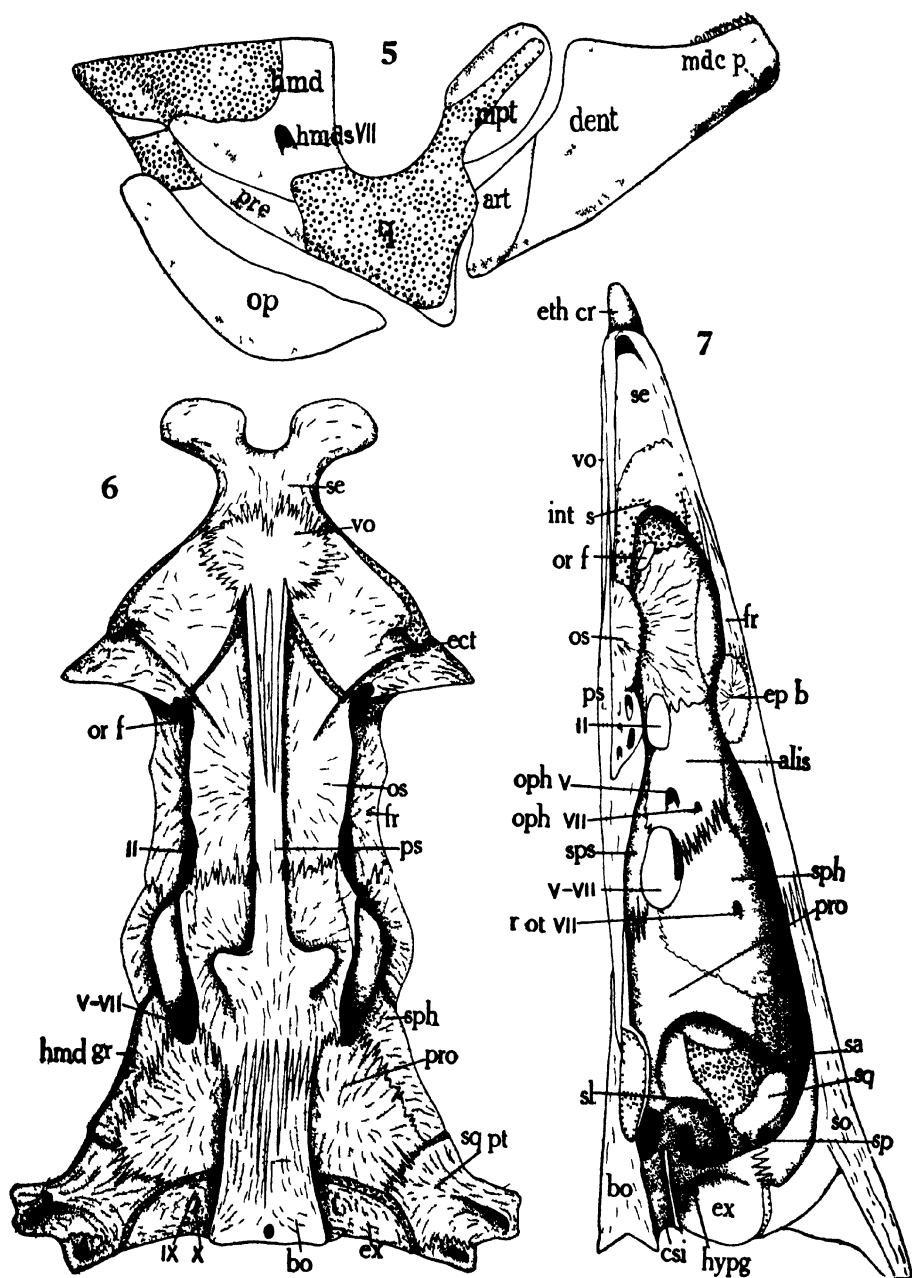
## EXPLANATION OF PLATE

Fig. 5.—Model of mandibular and suspensorial apparatus of 32 mm. *Amiurus*, lateral view; cartilage stippled.

Fig. 6.—Cranium of adult *Amiurus*, ventral view.

Fig. 7.—Same, median section and internal surface, cartilage stippled.

<i>alis</i>	alisphenoid bone	<i>or f</i>	orbital foramen
<i>art</i>	articulare	<i>os</i>	orbitosphenoid
<i>bo</i>	basioccipital	<i>pre</i>	preopercular
<i>csi</i>	cavum sinus imparis	<i>pro</i>	prootic
<i>dent</i>	dentary	<i>ps</i>	parasphenoid
<i>ect</i>	ectethmoid	<i>q</i>	quadrate
<i>ep b</i>	epiphysial bar	<i>r ot VII</i>	ramus oticus facialis foramen
<i>eth cr</i>	ethmoid cornu	<i>sa</i>	septum semicircularis anterius
<i>ex</i>	exoccipital	<i>se</i>	supraethmoid
<i>fr</i>	frontal	<i>sl</i>	septum semicircularis laterale
<i>hmd</i>	hyomandibula	<i>so</i>	supra occipital
<i>hmd gr</i>	hyomandibular groove	<i>sp</i>	septum semicircularis posterius
<i>hmds VII</i>	hyomandibularis branch of VII	<i>sph</i>	sphenotic
<i>hypg</i>	foramen for hypoglossus nerve	<i>sps</i>	supraorbital canal
<i>int s</i>	internasal septum	<i>sq pt</i>	squamos opterotic
<i>mdc p</i>	mandibular canal pores	<i>sq ptr</i>	squamoso-pterotic
<i>mpt</i>	metapterygoid	<i>vo</i>	vomer
<i>op</i>	operculum	<i>II</i>	optic foramen
<i>oph V</i>	foramen for ophthalmicus superficialis trigemini	<i>V-VII</i>	foramen trigemino-facialis
<i>oph VII</i>	foramen for ophthalmicus superficialis facialis	<i>I V</i>	glossopharyngeal foramen
		<i>X</i>	vagus foramen





## PLATE V

## EXPLANATION OF PLATE

Fig. 8.—Transverse section through middle of otic capsule and parachordal plate of 32 mm. *Amiurus*.

Fig. 9.—Posterior view of adult cranium of *Amiurus*.

Fig. 10.—Dorsal view of adult cranium of *Amiurus*.

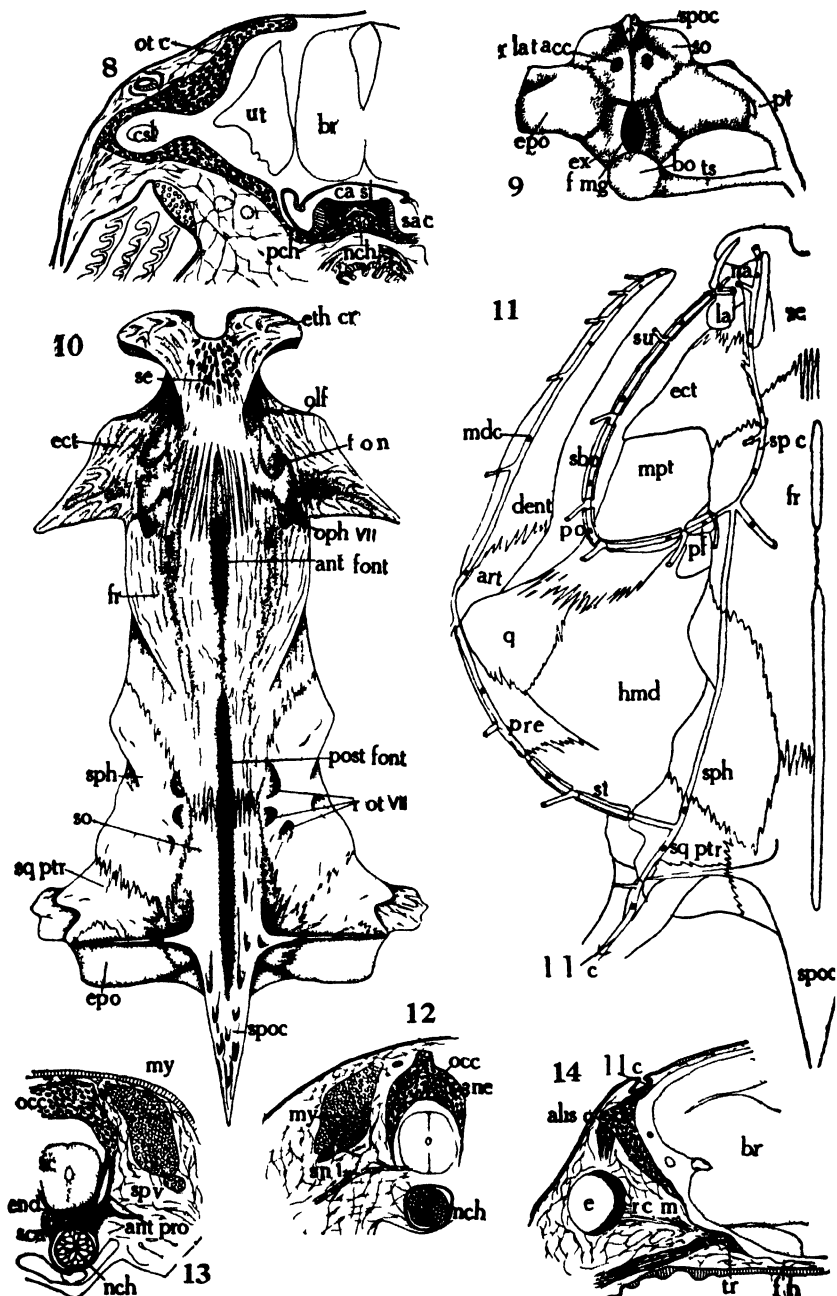
Fig. 11.—Dorsal view of adult cranium and jaws, showing diagrammatically the course of lateral line canal, position of pores and sense organs with regard to the bones.

Fig. 12.—Transverse section through the posterior part of the occipital arch of 8 mm. *Amiurus*.

Fig. 13.—Transverse section through the scaphia of an 8 mm. *Amiurus*.

Fig. 14.—Transverse section through posterior orbital region, 8 mm. *Amiurus*.

<i>alis c</i>	alisphenoid cartilage	<i>ot c</i>	otic capsule
<i>ant font</i>	anterior fontanelle	<i>pch</i>	parachordal
<i>ant pro</i>	anterior process of the scaphium	<i>pf</i>	postfrontal
<i>art</i>	articulare	<i>po</i>	postorbital
<i>bo</i>	basioccipital	<i>post font</i>	posterior fontanelle
<i>br</i>	brain	<i>pre</i>	preopercular
<i>ca si</i>	canal sinus imparis	<i>pt</i>	post-temporal
<i>csi</i>	lateral semicircular canal	<i>q</i>	quadrate
<i>dent</i>	dentary	<i>r lat acc</i>	ramus lateralis accessorius fa-
<i>ect</i>	ectethmoid		cialis foramen
<i>end</i>	endorhachis	<i>rc m</i>	rectus eye muscle
<i>epo</i>	epiotic	<i>r ot VII</i>	ramus oticus facialis foramen
<i>eth cr</i>	ethmoid cornu	<i>sac</i>	sacculus
<i>ex</i>	exoccipital	<i>sbo</i>	suborbitals
<i>f h</i>	fenestra hypophyseos	<i>sc</i>	spinal cord
<i>f mg</i>	foramen magnum	<i>sca</i>	scaphium
<i>f o n</i>	foramen orbito-nasale	<i>se</i>	supraethmoid
<i>fr</i>	frontal	<i>sn l</i>	first true spinal nerve, second post-vagal nerve
<i>hmd</i>	hyomandibula	<i>so</i>	supraoccipital
<i>la</i>	lacrimal	<i>spc</i>	supraorbital canal
<i>ll c</i>	lateral line canal	<i>sph</i>	sphenotic
<i>mdc</i>	mandibular canal	<i>spoc</i>	spina occipitis
<i>mpl</i>	metapterygoid	<i>s po</i>	saccus paravertebralis
<i>my</i>	myotome	<i>sq ptr</i>	squamoso-pterotic
<i>na</i>	nasal	<i>st</i>	subtemporals
<i>nch</i>	notochord	<i>su</i>	suborbital canal
<i>occ</i>	occipital arch	<i>tr</i>	trabecula cranii
<i>olf</i>	olfactory foramen	<i>ts</i>	transcopular
<i>oph VII</i>	foramen for ophthalmicus super-	<i>ut</i>	utriculus
	ficialis facialis	<i>3ne</i>	third neural arch





**PLATE VI**



## EXPLANATION OF PLATE

Fig. 15.—Cranium of adult *Amiurus*, lateral view.

Fig. 16.—Same, anterior end, ventral view, with vomer and parasphenoid removed.

Fig. 17.—Transverse section through occipital region of 8 mm. *Amiurus*.

Fig. 18.—Transverse section through ethmoid region of 8 mm. *Amiurus*.

Fig. 19.—Transverse section through roof of the anterior semicircular canal of 32 mm. *Amiurus*.

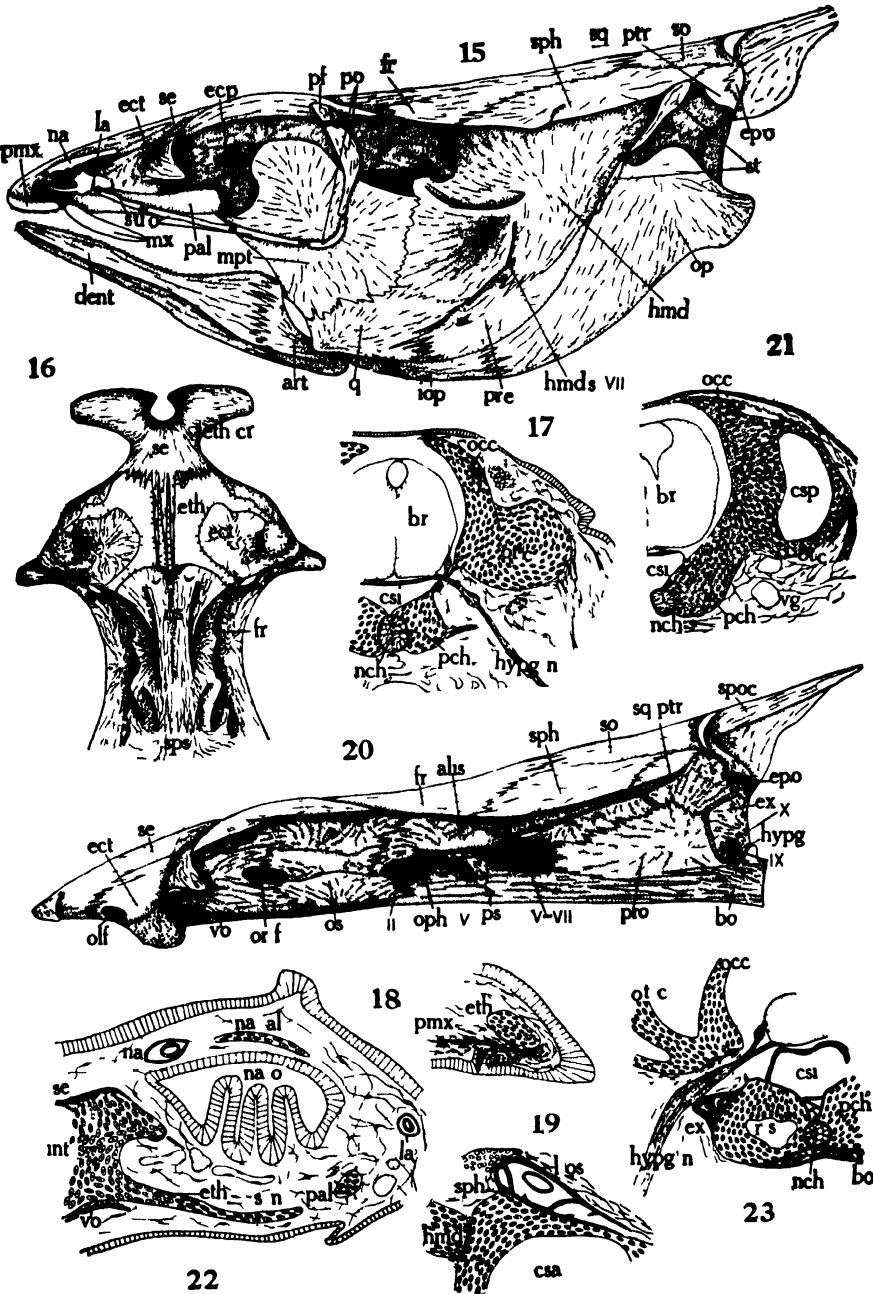
Fig. 20.—Adult cranium, lateral view.

Fig. 21.—Transverse section through fusion of occipital arch and parachordal plate, 8 mm. *Amiurus*.

Fig. 22.—Transverse section through anterior region of 32 mm. *Amiurus*.

Fig. 23.—Transverse section through the hypoglossal foramen of a 32 mm. *Amiurus*.

<i>alis</i>	alisphenoid bone	<i>oph V</i>	foramen for ophthalmicus super-
<i>art</i>	articulare		facialis trigemini
<i>bo</i>	basioccipital	<i>or f</i>	orbital foramen
<i>br</i>	brain	<i>os</i>	orbitosphenoid
<i>csa</i>	anterior semicircular canal	<i>ot c</i>	otic capsule
<i>csi</i>	cavum sinus imparis	<i>pal</i>	palatine
<i>csp</i>	posterior semicircular canal	<i>pch</i>	parachordal
<i>dent</i>	dentary	<i>pf</i>	postfrontal
<i>ecp</i>	ectopterygoid	<i>pmx</i>	premaxillary
<i>ect</i>	ectethmoid	<i>po</i>	postorbital
<i>epo</i>	epiotic	<i>pre</i>	preopercular
<i>eth</i>	ethmoid plate	<i>pro</i>	prootic
<i>eth cr</i>	ethmoid cornu	<i>ps</i>	parasphenoid
<i>ex</i>	exoccipital	<i>q</i>	quadrate
<i>fr</i>	frontal	<i>r s</i>	recessus sacculi
<i>hmd</i>	hyomandibula	<i>se</i>	supraethmoid
<i>hmds VII</i>	hyomandibularis branch of VII	<i>s n</i>	solum nasi
<i>hypg</i>	foramen for hypoglossus nerve	<i>so</i>	supraoccipital
<i>hypg n</i>	hypoglossus nerve	<i>sph</i>	sphenotic
<i>int s</i>	internasal septum	<i>spoc</i>	spina occipitis
<i>iop</i>	interoperculum	<i>sps</i>	suprasphenoid
<i>la</i>	lacrimal	<i>sq</i>	squamosal
<i>l os</i>	lateral line ossification	<i>sq ptr</i>	squamoso-pterotic
<i>mpt</i>	metapterygoid	<i>st</i>	subtemporals
<i>mx</i>	maxillary	<i>suo</i>	suborbital canal
<i>na</i>	nasal	<i>vg</i>	vagus nerve
<i>na al</i>	nasal alar cartilage	<i>vo</i>	vomer
<i>na o</i>	nasal organ	<i>II</i>	optic foramen
<i>nch</i>	notochord	<i>V-VII</i>	foramen trigemino-facialis
<i>occ</i>	occipital arch	<i>IX</i>	glossopharyngeal foramen
<i>olf</i>	olfactory foramen	<i>X</i>	vagus foramen
<i>op</i>	operculum		





## PLATE VII

## EXPLANATION OF PLATE

Fig. 24.—Transverse section through lower jaw of 60 mm. *Amiurus*, midway between symphysis and quadrate articulation.

Fig. 25.—Similar section, 32 mm. *Amiurus*.

Fig. 26.—Transverse section through the parachordal plate ventral to the vagus foramen, 32 mm. *Amiurus*.

Fig. 27.—Transverse section through anterior end of parachordal, 32 mm. *Amiurus*.

Fig. 28.—Same, a little farther posterior.

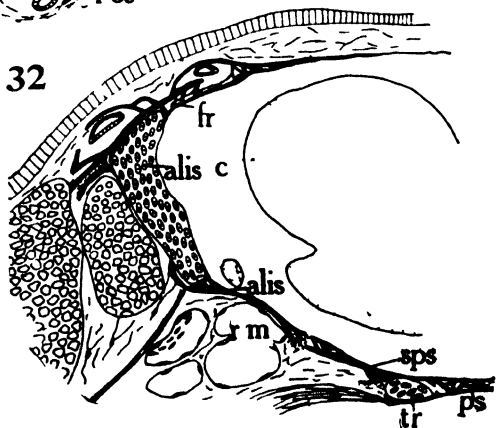
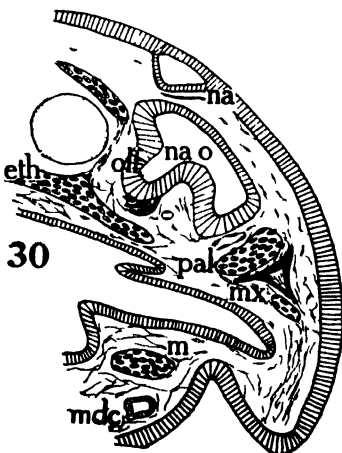
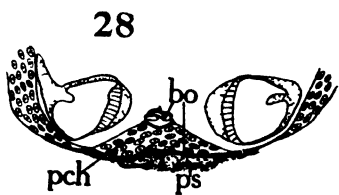
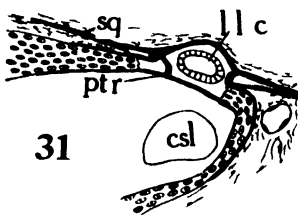
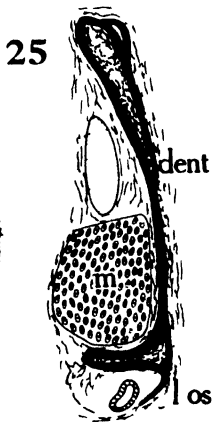
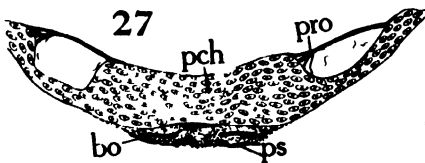
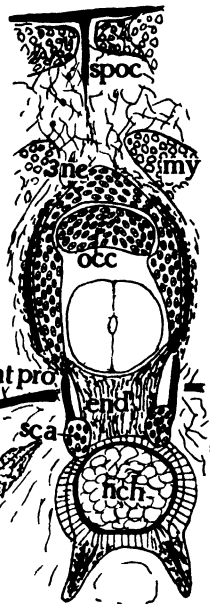
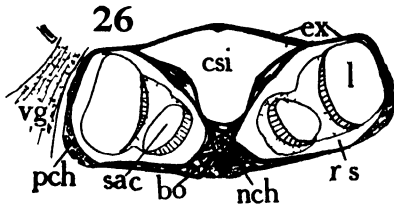
Fig. 29.—Transverse section through posterior part of occipital arch, 32 mm. *Amiurus*.

Fig. 30.—Transverse section through ethmoid region, 8 mm. *Amiurus*.

Fig. 31.—Transverse section through roof of lateral semicircular canal, 32 mm. *Amiurus*.

Fig. 32.—Transverse section through posterior orbital region, 32 mm. *Amiurus*.

<i>alis</i>	alisphenoid bone	<i>occ</i>	occipital arch
<i>alis c</i>	alisphenoid cartilage	<i>olf</i>	olfactory foramen
<i>ant pro</i>	anterior process of the scaphium	<i>pal</i>	palatine
<i>bo</i>	basioccipital	<i>pch</i>	parachordal
<i>csi</i>	cavum sinus imparis	<i>pro</i>	prootic
<i>csi</i>	lateral semicircular canal	<i>ps</i>	parasphenoid
<i>dent</i>	dentary	<i>ptr</i>	pteroic
<i>end</i>	endorhachis	<i>r m</i>	rete mirabile of the internal
<i>eth</i>	ethmoid plate		carotid artery
<i>ex</i>	exoccipital	<i>r s</i>	recessus sacculi
<i>fr</i>	frontal	<i>sac</i>	sacculus
<i>l</i>	lagena	<i>sca</i>	scaphium
<i>l l c</i>	lateral line canal	<i>sn l</i>	first true spinal nerve, second
<i>l os</i>	lateral line ossification		post-vagal nerve
<i>m</i>	Meckel's cartilage	<i>spoc</i>	spina occipitis
<i>mdc</i>	mandibular canal	<i>sq</i>	squamosal
<i>mx</i>	maxillary	<i>tr</i>	trabecula cranii
<i>my</i>	myotomes	<i>vg</i>	vagus nerve
<i>na</i>	nasal	<i>3nc</i>	third neural arch
<i>na o</i>	nasal organ		
<i>nch</i>	notochord		





## PLATE VIII



## EXPLANATION OF PLATE

Fig. 33.—Transverse section through the roof of the anterior end of the otic capsule, 60 mm Amiurus

Fig. 34.—Transverse section through the synotic tectum, 32 mm. larva.

Fig. 35.—Diagram of nerve, neural arch and myotome relations of a larval Amiurus.

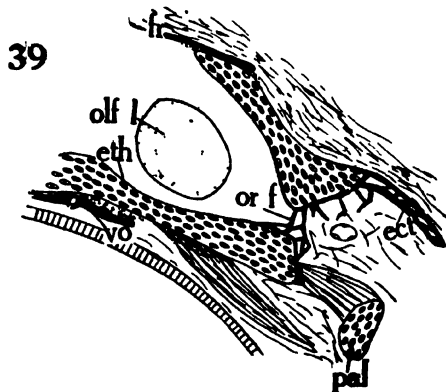
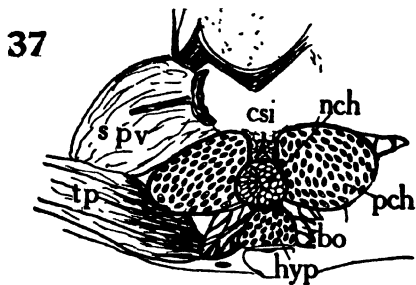
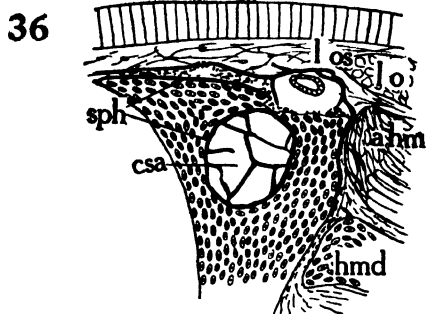
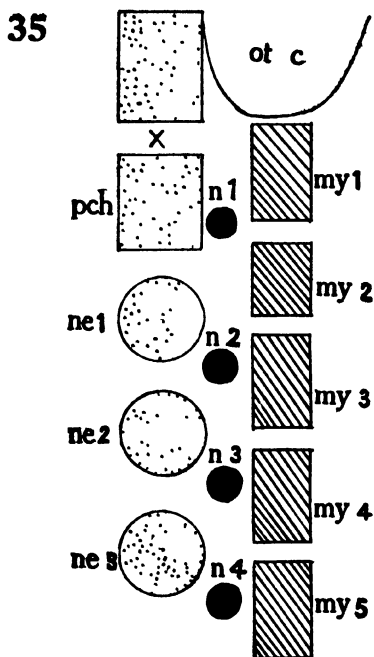
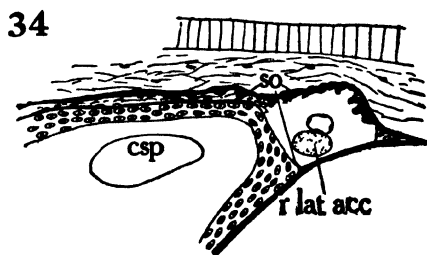
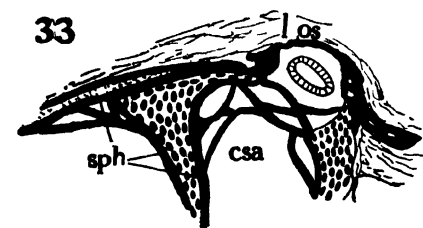
Fig. 36.—Transverse section through the anterior end of the anterior semicircular canal, 32 mm. Amiurus.

Fig. 37.—Transverse section through the posterior end of the basal plate, 32 mm. larva.

Fig. 38.—Transverse sections through the posterior end of the otic capsule, 32 mm. Amiurus.

Fig. 39.—Transverse section through the posterior part of the ethmoid region, 32 mm. Amiurus.

<i>a hm</i>	adductor, hyomandibularis	<i>nch</i>	notochord
<i>bo</i>	basioccipital	<i>ne 1-3</i>	neural arches 1-3
<i>csa</i>	anterior semicircular canal	<i>olf l</i>	olfactory lobe
<i>csi</i>	cavum sinus imparis	<i>or f</i>	orbital foramen
<i>csp</i>	posterior semicircular canal	<i>ot c</i>	otic capsule
<i>ect</i>	ectethmoid	<i>pal</i>	palatine
<i>epo</i>	epiotic	<i>pch</i>	parachordal
<i>eth</i>	ethmoid plate	<i>pt</i>	post temporal
<i>fr</i>	frontal	<i>r lat acc</i>	ramus lateralis accessorius facialis foramen
<i>hmd</i>	hyomandibula	<i>so</i>	supraoccipital
<i>hyp</i>	hypochordal cartilage	<i>sph</i>	sphenotic
<i>l o</i>	levator operculi	<i>s pv</i>	saccus paravertebralis
<i>l os</i>	lateral line ossification	<i>tp</i>	tubule pore of lateral line canal
<i>my 1-5</i>	myotomes 1-5	<i>vo</i>	vomer
<i>n 1-4</i>	post-vagal nerves 1-4	<i>X</i>	vagus foramen





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CONTRIBUTIONS TO THE LIFE  
HISTORIES OF *GORDIUS ROBUS-  
TUS* LEIDY AND *PARAGOR-  
DIUS VARIUS* (LEIDY)

WITH TWENTY-ONE PLATES

BY  
HENRY GUSTAV MAY

**THESIS**

**SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE  
OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE  
SCHOOL OF THE UNIVERSITY OF ILLINOIS**

**1917**

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## INTRODUCTION

The Gordiacea seem to have escaped the observation of the earlier writers or else to have been mistaken for filariæ. Meissner (1856) and Villot (1874) who review the older literature, agree that the first reference to the group was made by Albert the Great. Linnaeus introduced the term Gordius on account of the resemblance of a mass of the worms to the Gordian knot. He included in the genus the three species *G. aquaticus*, *argillaceus* and *medinensis*, representing respectively the present families of Gordiidae, Mermithidae and Filariidae, only the first of which is today retained in the order Gordiacea.

Dujardin was the first to give detailed descriptions of two species, *Gordius aquaticus* and *Gordius tolosanus*, and to point out the difference between Gordius on the one hand and Mermis on the other.

Von Siebold and following him Meissner (1855) placed Gordius and Mermis together to form the order Gordiacea. Meissner's work on the anatomy and physiology of Gordius and Mermis is in many respects an excellent production and it is inconceivable how, after such observations, he could still regard the two groups as closely related. The work of Grenacher (1868) on the anatomy of Gordius was a step in the right direction. He emphasized again the difference between Gordius and Mermis and stated that the two could not possibly belong to the same family.

Villot was the first to take up the study of museum specimens and living material in larger quantities. His investigations were carried on for a long series of years and with an earnest desire to solve the problems of taxonomy, physiology and life history; but unfortunately did not contribute much to a clearer knowledge of the group. The problem was too great for the methods he employed.

In England Baird described several species and in Germany von Linstow added a large number of names without giving descriptions adequate for identification.

The greatest contributions to the taxonomy of the group have undoubtedly been made by Camerano, chiefly because he had at his disposal more material than has ever been available to any other writer. He not only described a large number of species, but subdivided the group into several genera. Creplin (1847) had already established the genus Chordodes. Camerano (1897) carried the division farther in separating the genera Paragordius and Parachordodes from the genus Gordius. This separation was made purely on external characters. Montgomery in a paper coming out somewhat later also established a genus Paragordius which, so far as the anatomy of the forms is known, includes the same species as does that of

Camerano, but is founded on much more essential characters. That the genus has found universal acceptance is perhaps due more to Montgomery's characterization than to that of Camerano. The genus *Parachordodes* has not been universally accepted; but here again the evidence presented in this report shows that the characters given by Camerano are accompanied by others which indicate a natural division of the group. He characterizes *Gordius* by the presence of a postcloacal ridge in the male and the absence of true areoles on the cuticula, *Parachordodes* by the absence of postcloacal ridge and the presence of areoles.

In America several species were described by Leidy, but most of the systematic work was done later by Montgomery. Here as well as in Europe little more than pioneer work has been done. Descriptions and identifications have been made chiefly from preserved material and isolated specimens and only in a few cases from living material collected in abundance.

The confusion that still exists in the group is due in a large measure to the fact that the variations within a species are very great while the differences between species are relatively small. When isolated and often poorly preserved specimens are studied it is natural that essential characters are often overlooked and variations are taken for specific characters. This tends on the one hand to throw species together and on the other to separate members of a single species.

The two characters causing the most confusion are size and color. Nearly all of von Linstow's descriptions include besides these only those that are common to nearly all Gordiacea. Such descriptions are useless. I have in my own collection specimens of a single species ranging in length from 10 to 50 cm. and in color from light brown to nearly black and others that are an iridescent gray. Even as late as 1910 Wesenberg-Lund identified specimens as *Gordius aquaticus* on account of their size and made the errors that I shall point out later.

The light spots in the cuticula and the postcloacal ridge in the male have been taken as specific characters, and the species bearing either has usually without hesitation been assigned to *Gordius aquaticus*. The ridge certainly is possessed by more than one species and may be a generic character while the white spots, as Montgomery suspected, are due to physiological conditions in the American species but may be due to structures in the hypoderm in some of the European species.

Altho the structure of the cuticula is one of the best specific characters, its use has led to confusion because different authors have studied it under different conditions and have made different interpretations of what they saw. The erroneous theory that size, color and cuticular structures change with the age of the free living specimen has also contributed to the tangle.

The habits of different species are practically unknown. Most of the material has been found accidentally as isolated specimens and observations on behavior have been made mostly on animals in captivity as Wesenberg-Lund has already pointed out. The scant observations made on animals in nature are mostly referred to the group as a whole and not to any particular species. But there is no reason for supposing that the habits of different species are the same, and they are not the same in the species forming the subject of this paper.

The problem of the life history of the group has attracted much attention. Villot at one time thought he had the complete cycle, but found later that he had to modify his theories. He observed the embryological development, the encystment of the larvae in a large number of animals, and the presence of nearly adult worms in beetles. After holding for a long time the view that the animals harboring the encysted larvae were intermediate hosts he finally concluded that the encysted larvae perish and that the life cycle is completed in some other way. Camerano independently arrived at the same conclusion. Blunck (1915) again speaks of an intermediate host. He states that the larvae of *Gordius tolosanus* penetrate soft-bodied animals and these in turn are devoured by *Dytiscus* larvae. Tadpoles form for the most part the intermediate host. Development is completed in *Dytiscus* and the worms escape soon after the beetle emerges from the puparium. The facts upon which these deductions are based are not given. Nothing has been published on the metamorphosis or the structure of the early parasite. In regard to the later organogeny Villot (1891) and Vejdovsky (1894) have supplied the only information.

The adult organization is better known. If the knowledge of it is still incomplete, that is due chiefly to the fact that the material at hand has often been scarce and the methods employed have given only poor results. Here as elsewhere the greatest confusion has arisen because of the belief that what is true of one species must be true for all. Writers have not hesitated to denounce their fellow workers when their particular species failed to show what others had found in very different species.

This very brief discussion of the literature on Gordiacea has been given not with the purpose of presenting an historical account of the subject but with the object of pointing out the need for further investigation and some of the difficulties that have presented themselves.

The present investigation was undertaken with the object of increasing the knowledge of some of the common American Gordiacea. The chief purpose was to trace out if possible the complete life cycle in one or the other of the two species most easily available; special attention being given to the host succession and the organogeny.

The work was suggested in the fall of 1913 by Professor Henry B. Ward, under whose direction it was carried on. To him I wish also to express

my sincere appreciation for a keen interest in the work and for many helpful suggestions. Professor Ward also placed at my disposal his library and his collection.

Other material was obtained for study from Harvard University, the University of California and the University of Pennsylvania. Doctor Minnie Watson Kamm kindly donated an infected host collected in the vicinity of Urbana and containing valuable material of *Paragordius varius*.

The early collections were made under the direction of Professor Frank Smith, while the work at Douglas Lake, Michigan, was made possible thru the kindness of the director of the station, Doctor H. A. Gleason, and was carried on under the direction of Doctor W. W. Cort.

Many helpful suggestions were obtained from Doctor T. B. Magath and other workers in Professor Ward's laboratory.

#### MATERIAL AND METHODS

The two species studied are *Gordius robustus* Leidy 1851 and *Paragordius varius* (Leidy 1851).

*Gordius robustus* is well known in America; its range extends from the Atlantic to the Pacific. It is by far the most abundant species in the streams near Urbana, Illinois, and is occasionally picked up in collections made for the zoological laboratory of the University of Illinois. Eight males and one female were collected among dead grass at the water's edge in a small stream on March 25, 1914. Then, for nearly a month, diligent searches in similar localities were fruitless. On April 18 several more specimens were found.

It was noted at the time that both localities were at the edges of rapids. This led to the investigation of other rapids with the result that hundreds of specimens were collected. It was possible to walk along the bank of a stream and descend at rapids with grassy borders and collect *Gordius* in masses containing sometimes as many as 25 or 50 worms. Collections were made at short intervals until the middle of June. More material was collected in 1915 and 1916.

The material in the collection of Professor Henry B. Ward at the University of Illinois was available for study as well as Leidy's specimens of 1879 and the material from the collections at Harvard University and the University of California.

Eggs were found thruout the month of May and the larvae hatched the latter part of May and during June.

Parasitic stages were obtained in large numbers in the fall of 1914 and again in 1916. Earlier stages were obtained by infecting the hosts in the laboratory. About 500 specimens in different stages of development were obtained for the investigation.

*Paragordius varius* is even more abundant than the previous species and is the one most commonly collected in this country.

Several adults of this species were collected early in June of 1914. Hundreds of specimens were obtained at Douglas Lake, Michigan, during June, July and August, 1915, and a few more at Urbana in the spring of 1916. Material from the collections mentioned under *Gordius robustus* was also available.

Eggs and larvae were obtained in large numbers wherever adults were found.

Parasitic stages were obtained in the fall of 1914 from one host given to me by Minnie Watson Kamm, who was working on gregarines in this laboratory at that time. Abundant material was obtained in all but the very youngest stages in the summer of 1915 at Douglas Lake. Over 500 specimens were available for study.

The ordinary methods used in anatomical and histological study were found to be almost useless when applied to the study of the Gordiacea and special methods had to be adapted and devised at nearly all stages of the investigations.

The study of living material was confined mostly to field observations on adults and hosts and to the study of the embryonic development and larval structure. Nothing is gained by the study of the parasitic forms in the living condition.

For the removal of parasites from the hosts it was necessary to use a normal salt solution of full strength (0.75%). Even in this a slight injury usually caused a flowing out of part of the body contents. In pure water the specimens rupture at short intervals all along the body almost as soon as immersed. This applies of course only to the younger stages and not to those that have already formed the adult cuticula. The specimens were usually removed by tearing away the host tissues in salt solution by means of fine forceps or needles. For smaller specimens the host tissues were teased out in a watch glass and the contents examined under the low power of a microscope at a magnification of about 100 diameters.

The problem of the proper killing fluid was one of the most difficult to solve, and in part has not yet been solved. On account of the special methods of dehydration and imbedding it was impossible to test out quickly the action of any particular killing fluid and on account of the short seasons at which material was available such testing could usually not be done during the collecting season. It was necessary under those conditions to use the rapidity with which the killing fluid acts and the general appearance of the killed material as criteria. Most of the earlier material was killed in a saturated solution of corrosive sublimate to which from five to ten per cent of glacial acetic acid had been added. Later this solution was saturated with picric acid because with that modification it killed specimens more quickly and prevented to a great extent the rupturing of the parasitic forms in the killing fluid. But histological preparations show that this

fluid is inferior to plain corrosive acetic. Other killing fluids tried were Flemming's solution, Zenker's fluid, Kleinenberg's picro-sulphuric, formalin and other less known fluids. The best preparations so far have been obtained with corrosive acetic when the solution was used at a temperature of from 40 to 60° C. The glycerol-alcohol mixture recommended by Looss for killing nematodes yields specimens as flat as ribbons and bearing no resemblance to Gordiacea.

For killing infected hosts the solution of Carnoy and Lebrun consisting of equal parts of absolute alcohol, chloroform and glacial acetic acid saturated with corrosive sublimate was found to give very excellent results. It could not be used for killing Gordiacea because it made the material collapse nearly as badly as did the glycerol-alcohol mixture.

The methods of preparing the material for microscopic study were more easily devised as it was possible to take up this problem at convenience.

The ordinary methods of dehydration, clearing and imbedding were found to yield nothing but flattened, torn and distorted preparations. In delicate specimens at certain stages a sudden increase of one per cent in the concentration of the alcohol caused excessive flattening and distortion. It was therefore necessary to use an apparatus for insuring the gradual changing of the liquids in dehydrating and clearing. Several devices for this purpose have been introduced by European workers. The one best known in this country is the differentiator introduced by N. A. Cobb for making microscopic preparations of free living nematodes. This apparatus is made possible by the fact that successive layers of alcohol of increasing strengths can be introduced into a narrow glass tube without mixing. By stirring up the tube a little it is possible to obtain a column of alcohol gradually increasing in strength from the bottom upward. If the specimen is placed in the bottom of the tube and the alcohol permitted to ooze out thru a capillary point, it is possible to draw over this specimen a stream of alcohol of gradually increasing strength.

The apparatus used for this work depends upon a slightly different principle. When alcohol is introduced at the bottom of a broad tube filled with alcohol of a lower strength there is a certain amount of mixing of the two liquids. Such a tube can be used as a mixing chamber. The essential parts of the apparatus used consist of a reservoir, the mixing chamber and the specimen chamber. The reservoir is a tube about 2 cm. in diameter and 25 cm. long. It is supplied at the bottom with a rubber stopper thru which a piece of small glass tubing leads nearly to the bottom of the mixing chamber. The best results are obtained when this glass tube is drawn out so as to leave an opening of not more than 2 mm. at the bottom. The mixing chamber consists of a piece of glass tubing about 1.5 cm. wide and 5 cm. long supplied at each end with a perforated rubber stopper. From the bottom of this chamber a piece of narrow glass tubing leads to the top

of the specimen chamber. This tube must be bent in the shape of an S to raise the specimen chamber to a point where the outlet is above the lowest part of the mixing chamber to keep the apparatus from running dry. The same result can of course be obtained by inserting the specimen chamber under the mixing chamber and bending up the outlet tube to a point above the top of the specimen chamber.

This apparatus was for this work preferred to the Cobb type because it permitted the dehydration of a large amount of material at one time and so saved an infinite amount of labor.

When the specimens were dehydrated they were removed from the chamber into a small stendor dish and cleared in xylene by means of the string differentiator described by Magath. This consists essentially of three dishes placed one above the other like steps in a stairway. The upper dish contains the liquid to be introduced, the middle dish contains the specimens, and the lower one the waste. The liquid is transferred from dish to dish by means of string siphons. The string drawing the liquid from the specimen dish does not reach the bottom of that dish and so prevents the removal of all the liquid from the specimens when the upper dish goes dry. The whole apparatus is covered by a bell jar sealed at the bottom to prevent the alcohol from absorbing moisture from the air.

This differentiator was later adapted also for dehydrations. The chief objection to the use of the apparatus described by Magath for dehydration lies in the fact that the stronger alcohol introduced into the specimen dish tends to form a layer at the top and is drawn off again by the second string, increasing only very slowly the strength of the lower alcohol, causing an enormous waste of liquid, and usually ruining the specimens. It is possible to withdraw the alcohol from the bottom of the specimen dish by means of a capillary glass tube bent in the shape of a U. This capillary tube must widen out rather suddenly at the outlet to an inside diameter of about two millimeters and this end must be bent outward so that the liquid drops freely from the tube without touching the dish. If this tube is not widened at the outlet it is impossible to keep the alcohol in the specimen dish at the proper level on account of the different effect of capillarity on the different grades of alcohol. An ordinary capillary tube that will keep water at the proper level will drain the dish completely when the higher grades of alcohol are used. The level at which the liquid will be maintained is determined by the position of the outlet of the capillary tube as the liquid will stop flowing when the level tends to become lower and will start automatically when that level is raised. For clearing specimens dehydrated in this differentiator the capillary tube is replaced by a string. This apparatus is by far the most convenient and the safest for delicate specimens as they can be kept in the same dish thruout the entire process of dehydration and infiltration.



Specimens transferred from xylene to a solution of paraffin in xylene or from a saturated solution of paraffin in xylene to melted paraffin are usually injured by the appearance of gas bubbles in the tissues and consequent tearing and distortion. To avoid this the following method of infiltration was introduced. Pieces of solid paraffin are successively added to the xylene containing the specimens until the solution becomes saturated. When the solution is saturated at room temperature the dish is placed in a warming oven or on the top of the paraffin bath and the process continued till saturation is again reached. The infiltration to this point usually requires two to three days. The dish is now placed in the paraffin bath and the process continued rather rapidly until the solution becomes practically pure paraffin. The specimens are then transferred to pure paraffin and imbedded after about two hours. The entire period during which the specimens are left in the paraffin bath is usually not more than four hours.

For imbedding Gruebler's best paraffin with a melting point of 56 to 58° C. was found to give the best results. The ordinary paraffins were found to be either too soft or too brittle for this work. Parowax, the Standard Oil product on sale at nearly all groceries, would be an excellent medium if the temperature of the sectioning room could be kept down to about 15° C.

For sectioning specimens imbedded in the hard paraffin at ordinary room temperature it was necessary to dip the trimmed block into melted soft paraffin. After cooling the soft paraffin was removed from all sides except the lower. Blocks treated in that way, when sectioned 7 to 10 $\mu$  thick, produce beautiful ribbons in which the sections show no evident shrinkage or rolling.

All cross sections and most of the longitudinal sections were cut 7 $\mu$  thick. Longitudinal sections of specimens in which the adult cuticula had been formed had to be cut 10 $\mu$  and even then gave only poor results on account of the unequal expansion and contraction of different parts when the sections were cut. Cross sections of such specimens also showed distortions from the same causes. In younger specimens in which the cuticula was still soft the sections could be flattened out fairly well by placing them on water on a slide and warming the slide suddenly to the point where the paraffin began to become clear but did not become completely melted. Even with that treatment the cuticula often retained a wavy outline not normal to the living specimen. For later stages the warming usually had to be continued until the paraffin was completely melted. Good results were obtained with such specimens when the slide was placed in the paraffin bath for half an hour or more until the water had evaporated from under the ribbons. For that purpose the bath must be warm enough to melt the paraffin as otherwise blistering takes place and the sections may be ruined.

In all cases the sections were fixed to the slide by means of Meyer's albumen fixative. Slides containing older specimens had further to be treated with a very thin solution of celloiden while transferring from absolute alcohol to 95% before staining.

In sectioning adults the friction between the specimen and the knife often caused the ribbon to become highly charged with static electricity. This was especially true of specimens that had become excessively hardened in the process of dehydration and infiltration. The only remedy was to trim the block less closely and make sure that it was properly treated with soft paraffin. The same rules had to be followed in sectioning crickets and grasshoppers.

The best stain was found to be iron hematoxylin. Unna's polychromatic methylene blue method with orcein as a counter stain gave fair results, Mallory's connective tissue stain was useful for demonstrating basement membranes; Delafield's hematoxylin, Ehrlich's hematoxylin and the carmine stains gave very mediocre results.

The iron hematoxylin method had to be modified according to the developmental stage and condition of the material, and the structures to be shown. For mordanting a 4% solution of iron ammonia alum was used and for staining a 0.5% solution of hematoxylin in water. Sections were usually mordanted about twice as long as they were stained except in case of very short staining periods when they were mordanted about half an hour.

Older parasitic stages were usually stained from half an hour to one hour, adults from one to two hours or for nerve structures from six to twelve hours, younger stages for very short periods, sometimes not more than thirty seconds. Destaining was nearly always done in a saturated solution of picric acid in water. This was found to take the stain out more uniformly than did the iron alum.

For counterstaining the slides were left for from twelve to twenty-four hours in xylene to every fifty cubic centimeters of which had been added three to five drops of a saturated solution of eosin in absolute alcohol. Fresh eosin must be added from time to time as it precipitates very rapidly unless there is a large amount of alcohol in the xylene.

## OBSERVATIONS ON GORDIUS ROBUSTUS

Since the investigation was begun on *Gordius robustus* Leidy and since the series of observations is most complete in this species, it is but natural that it should form the first part of the discussion.

## DETERMINATION OF SPECIES

On account of the confusion existing in the literature in regard to this and related species it is necessary to take up at this point a precise characterization of the species and a determination of its position in the group. The species was named by Leidy in 1851 and specimens were again referred to it in 1879. The single female of 1851 has not been preserved but the specimens of 1879 have fortunately been kept in fair condition. Leidy's early characterizations are not sufficient for identification but his description of 1879 is fairly complete and the material is available for study. Montgomery has given a somewhat detailed description of the species, but he overlooked one of the most essential characters, the dorsal and ventral bands. Only a general description of the species will be given at this point, details of the structure being left for the discussion of the adult morphology.

*Dimensions.* Of the specimens collected near Urbana the females vary in length from 100 to 470 mm. and the males from 120 to 420 mm. The diameter of the females ranges from 0.5 to 1.25 mm., that of the males from 0.3 to 0.75 mm. Some of Montgomery's specimens from California are considerably larger. The females in Leidy's collection are very short and thick.

*Form.* Both males and females are cylindrical, decreasing very slightly in diameter toward the ends, the females more than the males. The shape of the anterior end is essentially the same in both sexes. In the average specimen the end is rounded in the shape of a hemisphere, separated from the body by a very slight constriction and of the same diameter as the body just behind the constriction (Fig. 27). In very stout-bodied females there is no trace of a constriction and the body becomes distinctly attenuated just before the end. This condition is at its extreme in case of the short, thick females in Leidy's collection (Fig. 28).

The posterior extremity of the female is slightly enlarged in the shape of a bulb and abruptly truncated at the end (Figs. 25, 26). The cloacal aperture is located at the center of the truncated area and there is no trace of a dorso-ventral furrow (Fig. 34).

The posterior end of the male bears two short, stout prongs (Figs. 8, 32). The length of the prongs varies somewhat, but is usually not much more than half the diameter of the body. Each prong is of conical shape with a slight flattening on the inner side. The body attenuates rapidly dorso-ventrally at the base of the prongs so that the diameter of the latter is less than half that of the body (Fig. 24). On the ventral side, a short distance anterior to the bifurcation is a crescent-shaped ridge with the ends of the crescent passing slightly onto the bases of the prongs. I have usually found this ridge to be a broad, open crescent and not U or V-shaped as represented in most of Montgomery's figures. The anus is located a short distance anterior to the middle of the crescent, almost at its very base.

*Color.* The usual color is light brown, but specimens vary from nearly white to nearly black and females that have deposited their eggs are gray. When light is reflected in the proper way the cuticula shows a distinct iridescence, very pronounced in females after deposition of the eggs. Such females examined in the sunlight present brilliantly all the colors of the rainbow. Ordinarily the iridescence gives the body of the worm the appearance of being longitudinally corrugated. The anterior end is clear white followed by a ring of dark brown which passes rather abruptly into the normal brown of the body. At the center of the anterior white area is often found a black spot indicating the position of the mouth (Fig. 33). Passing backward from the dark ring are two bands, one ventral and one dorsal, slightly darker than the rest of the body (Figs. 26, 27, 28). These bands can usually be traced to the posterior end of the female, but are more difficult to trace in the male. Even there the dorsal line can often be traced to the base of the fork while the ventral line disappears a short distance before the anus. Montgomery does not mention these lines or bands in his description of the species, but I have found them present in all of his material that I have examined as well as in Leidy's material. They are mentioned by Leidy in his description of 1879. In the female the cloacal opening is situated at the center of a dark area, which itself is surrounded by an area slightly lighter than the body color, and around that is a brown circle, the dark color of which passes more or less gradually into the general body color (Fig. 34). In the male the crescent is dark brown, almost black, and there is a small dark area surrounding the anus (Fig. 32). Lighter spots scattered over the body may or may not be present. I have found them on many specimens at Urbana (Fig. 16), but never as pronounced as in Montgomery's specimens from California.

*Cuticula.* The cuticula never shows any traces of areoles. Under low magnification it appears to be divided into rhomboidal areas, while higher magnification shows a system of finer intersecting lines (Figs. 4, 5). The white area at the anterior end is of more homogeneous structure. Bristles or hairs are present over the entire body. Montgomery says they are

branching, but I have been unable to find any branching forms and, from the manner in which they develop, I do not believe that branching forms occur in this species. The branching forms probably occur on some other species that Montgomery regarded as identical with this. The bristles are more abundant at the two ends. In the males on the outside of the prongs they are slightly longer than elsewhere and usually curved, while on the inner surfaces there are very short, conical setae (Figs. 121, 122, 123). No special bristles are located around the anus of the male (Figs. 96, 97, 98).

*Eggs and larvae.* In nature the eggs are laid in thick cords which break up into pieces seldom more than 10 to 15 mm. long and of a diameter nearly equal to that of the worm. The larva belongs to the type with a single terminal spine at the posterior end. In the newly hatched larva (Fig. 20) the body is about twice as long as the proboscis but later becomes much reduced (Fig. 14).

Montgomery at first referred this species to *Gordius aquaticus* var. *robustus*. Later he regarded it as *Gordius villoti* and eliminated the variety. It belongs to the group known by most European writers as *Gordius aquaticus*. The identification is usually based on Villot's description of what he regarded to be Dujardin's *Gordius aquaticus*. Rosa regarded the identity of the two species as impossible or at least highly improbable and called Villot's species *Gordius villoti*. At the same time he redescribed the species, basing his description on a male and two females. He found on the surface irregularly polygonal areolae which it is difficult to interpret as the rhomboidal areas in the cuticula. Villot later called them pseudoareolae and he as well as Camerano included them in the description of *Gordius aquaticus*, stating that they are not present in all specimens. Of Rosa's specimens only the male possessed the dorsal and ventral bands and the character is not included in the original description of Villot's species. It is however mentioned in the description of Dujardin and Villot's later descriptions. I have never found the bands absent on any specimen of *Gordius robustus* or *Paragordius varius* and believe the character is not variable within a species. On account of this and other differences between the male and females described by Rosa it seems certain that he included at least two species in his description, and it is possible that neither of them was identical with Villot's species.

Rosa believes that Villot's species can not be identical with that of Dujardin because Dujardin's description mentions pores 0.006mm. in diameter in the fibrous cuticula which Villot does not mention. On the other hand Villot mentions a dark collar behind the white anterior end, a postcloacal crescent in the male and clear spots in the cuticula not mentioned by Dujardin. Villot in 1886, however, does describe pores in the fibrous cuticula which he claims may attain the diameter of 0.006mm. On the other hand Dujardin describes clear areas 0.06mm. in diameter which he

regarded as openings in the homogeneous cuticula. Furthermore, since the dark collar is almost universally present in Gordiacea of this group, it is probable that it was not actually lacking in the specimen of Dujardin; and the fact that he overlooked this leads also to the possibility that he overlooked a crescent that may have been present. The latter assumption is moreover justified because there is at present no form known with a cuticula that is devoid of true areoles and in which the male possesses no crescent. Indeed Camerano makes the combination of presence of crescent and absence of areoles a generic character. The use of the name *Gordius aquaticus* by Villot seems justified in the light of these considerations. But his description probably includes a group of closely related species which some future investigator in Europe may be able to separate.

Since there are several characters ascribed by various authors to the European species that are not present in *Gordius robustus* the two species can not be combined. Among the characters not present in *Gordius robustus* are pseudoareolae, pores in the cuticula, a dorsoventral furrow at the posterior end of the female, and groups of cells extending from the hypoderm into the cuticula as described by Camerano (1888) and Rauther (1905). The larva, also, of the European form appears to have a shorter body than that of the American species.

It is difficult to see why Montgomery assigned the American species to *Gordius villoti*, since he himself states that Leidy's descriptions are sufficient to establish the identity of the species and he had Leidy's material at hand for additional information if necessary; furthermore, he certainly was aware of the fact that Leidy's first description was given in 1851 and his second description in 1879, while that of Rosa did not appear until 1882.

#### HABITS OF ADULTS

*Gordius robustus* emerges from its host during September and October and possibly the latter part of August. Specimens may then be found swimming freely in the streams or stranded at the water's edge. It is at this time that they are most easily obtained in general collections. But the period of migration does not last very long as the specimens soon become entangled in the grass and debris along the edge of the water.

During November and December I have still succeeded in finding specimens in the grass just below the level of the water in small brooks. Even at this time they tend to accumulate at or just below rapids. During January and February I have made no collections, but the latter part of March, when the ice has gone, specimens are again found in the grass. At that time I have usually found them deeper down, entangled in the roots of the grass even several inches in the ground.

During April and early May there seems to be another migration on the part of some of the worms, but I have never found them free in the water. Since worms in captivity will usually remain quiet during the day

but become active during the early part of the night it is probable that migrations in the streams occur at that time. By the middle of May all the worms seem to have accumulated among the roots of grass in or at the edges of rapids.

It is likely that copulation does not ordinarily take place during the fall migration, as specimens at that time are usually found isolated and seem to remain more or less isolated during the winter. During the spring migration, however, they gather together in large numbers and I have several times found females that still retained the mass of spermatozoa at the posterior end, showing that copulation had taken place not more than three days before. It is soon after this migration that egg-laying begins.

The process of copulation is not difficult to observe. If two fresh worms, male and female, are placed in a glass cylinder about 10 cm. in diameter, filled with water, copulation takes place in a short time and may be observed thru the walls of the cylinder. When specimens are placed in a large open dish they swim about actively for a long time and copulation usually does not take place until the latter part of the night, when they become more quiet, and sometimes not until the second night. For the observations for this report I used specimens that had just emerged from their hosts, but in early spring collections most of the females copulate after being brought to the laboratory and observations could easily be made on them. In spite of the fact that egg-laying does not seem to take place in the fall, the specimens are mature for copulation when they emerge. I have kept males and females that had just emerged or had been removed from the hosts in open dishes and had copulation take place within 48 hours after emergence.

There seems to be no definitely directed effort on the part of either male or female to seek its mate. There is of course the usual tendency on the part of both to become entangled with the other, but the solid knot that makes observation impossible is usually not formed by two specimens until they have been together for a long time. The two worms merely become intertwined at places and then again disentangled, only to become reentangled again. That process is continued until finally the body of the female comes to lie within the spiral coil formed by the posterior end of the male. This coil soon tightens, the prongs are spread over the body of the female (Fig. 30), and the posterior end of the male with a rotary motion passes backward over the body of the female. The male does not seem to choose the direction in which it is to move except that it tends to move contrary to the motion of the female. The direction taken is nearly as frequently toward the anterior end of the female as toward the posterior end. Usually after several trials the posterior end of the male passes over the posterior end of the female. When the prongs have already passed over the end (Fig. 31) a discharge of sperm takes place. The cloacal open-

ings of the two specimens are not superimposed at this time and the sperm mass does not enter the body of the female but adheres to the outside. The discharge usually lasts not more than thirty seconds and during this time the male continues to rotate on the body of the female. The sperm seems to be fluid when it leaves the body of the male but soon solidifies. Some is lost in the water.

The sperm mass (Figs. 10, 113) disappears from the female within two or three days. Most of the spermatozoa pass into the seminal receptacle. The mass is so tough that it is almost impossible to crush it in order to make a microscopic preparation and it does not seem possible that many spermatozoa are brushed off. The migration into the seminal receptacle is probably passive, as the spermatozoa show no movement when placed on a slide.

The first eggs appear the latter part of April and laying continues until early June. The eggs are deposited while the worms remain entangled in masses among the roots of grass. They are laid in thick cords about 0.5mm. in diameter and break up into short pieces from 5 to 30mm. long. When fresh they are pure white, but soon become discolored by the surrounding earth. They do not adhere very strongly to each other and are easily crushed under a cover glass for microscopic examination.

After the deposition of the eggs the adults soon become inactive and begin to die and disintegrate in parts. One may actually find females with the anterior end dead and disintegrated so that nothing but the cuticula is left while the posterior end is still depositing eggs. More commonly, however, disintegration does not appear until all the reproductive products have been discharged and it may begin at any part of the body or the whole specimen may die at once. Males usually die a week or two earlier than do the females. Most of the specimens are dead by the middle of June.

#### EARLY DEVELOPMENT

Since Montgomery in 1904 gave a detailed account of the development of the larva of *Paragordius varius* it seemed only of minor importance to repeat his work on some other species and consequently little attention was at first given to the embryology of this species. The observations that were made, however, show that not only the larval development of *Gordius robustus* but also that of *Paragordius varius* requires further investigation. It has not been possible to undertake that investigation for the present report.

To fill out the gap I shall give a very general account of the larval development of *Paragordius varius* as described by Montgomery. The eggs are fertilized in the cloaca and the two polar bodies are given off soon afterwards. The cleavage is total and adequal and soon forms a coeloblastula which early passes over into a typical gastrula. Mesenchyme is formed by the separation of cells from the invaginated entoderm. At the



end opposite the blastopore the ectoderm thickens and forms a second invagination, that of the proboscis. The entire proboscis develops from ectoderm except for a few mesenchyme cells which have migrated into it to form the muscles. The blastopore becomes nearly closed and the anterior end of the intestine does not communicate with the cavity of the proboscis during the embryological stages.

The description of the larva also can be given only in the most general terms at this time. The larva of *Gordius robustus* differs greatly in form from that of *Paragordius varius*, but in essential structures the two do not seem to differ much. The newly hatched larva (Fig. 20) is very much elongated, but after a week or so it has become shrunken to about half its original length (Fig. 14) and has increased slightly in diameter. Like all other known *Gordius* larvae it consists of proboscis and body. The proboscis is armed in front with three retractile stylets and at the sides with three circles of hooks which point backward when the proboscis is extended, but are withdrawn into the proboscis when this is retracted. A set of retractor muscles is inserted at the base of the stylets and protractors lie close to the outer wall of the proboscis. The body in the newly hatched larva is at least twice as long as the proboscis and of a slightly smaller diameter. Both body and proboscis are covered by external, more or less irregular cuticular rings which do not seem to be in any way related to the deeper structures of the larva. The posterior end of the body runs out to a point resembling a heavy spine. Between the proboscis and the body there appears to lie a partition separating the end of the intestine on one side from a cord of cells coming from the base of the stylets on the other. Just behind this partition is a mass of cells belonging to the intestine which farther back has very thin walls and encloses within its lumen two elongated masses of a homogeneous, highly refractive substance. Montgomery figures similar masses in the intestine of *Paragordius varius* and regards them as excretory waste. In *Gordius robustus* these masses are later absorbed as large cells invade this region. The intestine opens at the posterior end on the ventral side somewhat anterior to the spinelike elongation.

Beginning near the proboscis and extending backward two-thirds of the length of the body on the ventral side are two rows of nuclei indicating the rudiments of the ventral nerve cord. Only longitudinal muscles appear to be present in the body and they adhere so closely to the outer wall that it is difficult to detect them.

When fully developed the larva ruptures the egg-membrane and escapes from the egg-string by means of the armature of its proboscis. Quite active at first, it becomes more and more sluggish as it grows older. Larvae picked up with a pipette from the bottom of the dish containing the eggs usually show only a few active forms. If among a number of larvae in an open drop on a slide about ten per cent are active, then when a coverglass

is placed over the drop about half of the specimens will become active within five or ten minutes. The reaction is not due to pressure as the larvae can easily stand on end in the ordinary film of water. It may be a reaction to the lack of oxygen or the presence of carbon dioxide in the water.

The larvae bore their way into any animal tissue that happens to be accessible at the time. Villot was the first to discover this, and since he regarded all these animals as true hosts of the parasite, he stated that *Gordius* has no specific hosts. Later Villot himself, Montgomery and others found that the larvae merely encyst in most of these animals and are unable to undergo further development.

#### PARASITISM

With the entrance of the larva into the proper host begins one of the most important phases of the life cycle, the period that leads thru growth and differentiation to the formation of the mature worm.

The final and perhaps the only hosts of *Gordius robustus* I have found to be members of the grasshopper family Locustidae. The most common host around Urbana is *Orchelimum vulgare* Harris, but *Orchelimum nigripes* Scudder and *Xiphidium nemorale* Scudder seem to be equally heavily infected tho less common, and I have obtained two adult parasites from a female of *Scudderia furcata* Brunner. Over 100 specimens of *Xiphidium fasciatum* (DeGeer) from localities in which *Orchelimum vulgare* was heavily infected were examined but no infection was found. Over 200 specimens each of *Melanoplus differentialis* and *Melanoplus femur-rubrum* from similar localities also proved to be not infected. Large numbers of *Gryllus assimilis* and *Nemobius fasciatus* examined in the investigation on *Paragordius varius* were also not infected with *Gordius robustus*. Many aquatic insect larvae were also examined, but no infected specimens were found. From two to three percent of the crickets and grasshoppers examined were found to be infected with Mermithidae.

An intermediate host is not necessary. If one occurs in nature it can be nothing more than a carrier in which the larva undergoes no change. Evidence presented later shows that a larva that has begun to change into the parasitic form can not undergo a change of hosts without being destroyed in the process. Furthermore, I have succeeded in producing in the laboratory an infection of at least fifty per cent in Locustidae collected in a locality in which later collections showed that no infection occurred in nature.

I 1. On July 6, 1916 forty-one young Locustidae, mostly *Xiphidium fasciatum* and *Orchelimum vulgare* were infected by injecting a drop of water in which larvae of *Gordius robustus* were suspended into the abdomen by means of a capillary pipette made of hard glass. From counts made on similar drops of the suspension placed on a slide under the microscope it

was estimated that from five to ten larvae were injected into each host. On account of the unfavorable conditions under which they were kept most of the hosts died in the next few days. On the ninth, six of the infected hosts were killed, the tissues teased out in salt solution and the sediment examined. Two active larvae of *Gordius robustus* were found, both showing signs of having begun their development. Both were lost in an attempt to stain and mount them. On July 11 all hosts were dead except five. When these were examined as before, four somewhat older, but still active larvae were found. They also were lost by accident.

I 2. Suspensions of larvae of *Gordius robustus* were injected into the mouths of eleven young Locustidae on July 6. All died within a few days.

I 4. Four young specimens of *Orchelimum vulgare* were infected as in I 1 on July 9. On July 15 three of the specimens were examined and all were found to be infected, yielding four small parasites (Figs. 9, 11). The other host died.

I 7. On July 11 fifty-three Locustidae mostly by *Orchelimum vulgare*, which had become easily recognizable by this time, were infected as before. Specimens of this lot were killed for sectioning, at first every day and later every two days. On July 15 an adult was examined but nothing found. Another adult was killed and examined on July 22 and found to contain three young worms, the longest being about 10mm. in length and the smallest one about 5mm. On the following day the last three hosts were examined and all were found to be infected, yielding 11 parasites ranging from 3 to 10mm. in length.

I 8. On July 14 seventy-eight Locustidae, mostly young *Orchelimum vulgare* were infected. Some of these were again killed for sectioning and staining as were those of I 7. One adult host was examined on July 22 and found to be infected with one young parasite (Fig. 15). An examination of ten more hosts on the following day yielded only a single parasite about 2mm. long in the coiled stage. On August 11 the last two specimens were examined. Only one was infected and contained two parasites 25 and 30mm. long respectively.

Later infection experiments proved less successful. Of 45 control hosts not one was found to be infected.

Of the specimens preserved for sectioning only seven from I 7 have been thoroughly examined and six were found to be infected. Sections of some of the specimens found are shown in figures 47-49 and 50-55.

The results of these infection experiments show conclusively that an intermediate host is not necessary for *Gordius robustus*.

Infection in nature must begin in late June or early July and end the latter part of July or in August. The young of *Orchelimum vulgare* collected early in July were still small and could not have hatched more than a week or so before they were collected. By the middle of September most of the parasites are well along in their development.

TABLE I  
RESULTS OF INFECTING *Orchelimum vulgare* WITH LARVAE  
OF *Gordius robustus* IN THE LABORATORY

Exp. No.	Date in 1916	No. Inocu- lated	Examined							
			Fresh				Slides			
			No.	Inf.	Par.	Not Inf.	No.	Inf.	Par.	Not Inf.
I 1	Jy. 6	41	11	?	6	?				
I 4	9	4	3	3	4	0				
I 7	11	53	5	4	14	1	7	6	7	1
I 8	14	78	13	3	4	10				
I 10	22	16	16	0	0	16				
I 11	23	15	9	1	1	8				
Control			45	0	0	45				

Infection takes place at or near the place where the larvae have hatched. In the spring of 1914 *Gordius* was very abundant in all of the streams at which collections were made. Later all specimens of *Orchelimum vulgare* collected near these streams were equally and heavily infected. During the summer of 1915 the streams were continually flooded and, judging from the scarcity of *Gordius* in the fall of that year and the following spring the infection must have been very light. The only place where any appreciable infection can have taken place is a stream north of the city which ordinarily goes dry during the summer months. It was in that locality that adult worms were found in the spring of 1916 and the Locustidae were found to be heavily infected later in the summer. The stream west of Champaign which had supplied the major part of the material in 1914 is bounded by narrow, steep banks and the high water must have prevented the grass from growing in the bed of the stream as usual. This stream is also becoming more and more polluted with sewage and other refuse. Of 453 specimens of *Orchelimum vulgare* collected along the bed of this stream August 28 to September 4, 1916, only six specimens or 1.5 per cent were found to be infected. I had not succeeded in finding any specimens of *Gordius* in the stream the previous spring. Of 555 specimens of Locustidae collected in the bed of the stream north of Urbana along the distance showing the heaviest infection 110 specimens or about 20 per cent were infected and yielded 164 parasites while in the other collection no host had more than one parasite. A collection of 143 hosts along the same stream, but starting where the previous collection had left off, contained 8 infected specimens or 6 per cent and only a single parasite was found in each host.

These data show that infection is local to a high degree and consequently that infection must take place at the point where the larvae occur; in other words, that the larvae are not widely distributed by an intermediate carrier. The data also show that the host itself does not ordinarily migrate very much during the summer. The migration of the average host seems to be limited to a radius of about half a mile, perhaps less.

Just how the larva enters the host I have not been able to discover. In the spring of 1914 when the infection was so heavy I had not yet discovered the host and in the two succeeding years the infection was ordinarily so low that an attempt to work out that particular phase of the problem by observation in nature would have been a waste of time.

It will be sufficient here to give a brief account of the habits of the hosts, leaving the discussion of the possible modes of infection to be taken up later. Altho the species of *Orchelimum* and *Xiphidium* found to be the hosts of *Gordius robustus* are the common meadow Locustidae, they are much more abundant in the tall grass near the water's edge than elsewhere. *Orchelimum vulgare* and *Orchelimum nigripes* are found most abundant right at the water's edge while *Xiphidium nemorale* is more abundant on the taller weeds or on the banks of the streams.

The species are omnivorous but feed chiefly on grass and weeds. Several times I have found *Orchelimum vulgare* feeding on other insects. In captivity all of the species are cannibals, feeding on each other even when in larger cages. The collected grasshoppers had to be brought home in tightly stoppered bottles in which the oxygen supply soon became so low that the insects became quiescent, and even then they often injured each other severely before they could be brought to the laboratory and examined.

Tho the species are so abundant on the grass near the border I have never seen them deliberately entering the water. But their behavior differs so greatly during the different times of the day that it is possible for them to enter the water regularly at some time during the night or early morning but never do so during the time at which my collections were made. The specimens are most active during the early part of the day, especially when the sun shines. Since all specimens were collected by hand, simply by approaching slowly and grasping them suddenly, it was almost impossible to get specimens during the forenoon or early afternoon of a hot, sunny day. Altho on such days the males are singing everywhere, they become aware of the approach and drop to the ground long before they are in reach. Contrary to the habits of the Acrididae, these Locustidae never leap from place to place to escape an enemy, but drop down almost perpendicularly to a lower level in the grass or even to the ground. They either remain quiet where they drop or run along for some distance and then remain quiet so that it is almost impossible to find them. When situated on the

grass over the water they do not hesitate in the least to drop down into the water and are in no haste to get back to land. On cloudy days the specimens often remain at the bottom of the grass and can not be obtained at all, but on bright days, when it is just cloudy enough for the sun to be shaded, many of them come up and are easily obtained because they are less active than on sunny days. I have been able to obtain them most easily at twilight just after sunset. At that time they come out on the grass and weeds and do not easily become aware of approach, and even when disturbed they often merely run along to a new position without making any serious attempt to escape.

The larvae at first penetrate the adipose tissues of the hosts, making their way not only between the cells but also thru them (Figs. 47, 54).

In later stages they come to lie free in the body cavity of the host (Fig. 55). There is usually a difference in the location in the host between the Mermithidae and Gordiacea. While the Gordiacea occupy exclusively the body cavity, the Mermithidae usually penetrate the tissues surrounding the body cavity and sew themselves thru between the muscle bundles of the thorax. Whenever *Gordius* becomes too crowded in the abdominal cavity and is forced into the thorax it passes between the alimentary canal and the thoracic muscles, but never between the muscle bundles.

The parasite does not appear to impair very greatly the health of the host, for, unless the infection is very heavy, the infected specimens appear to be just as active as those that are not infected. In this respect the infection differs from an infection with *Mermis*. I have several times found specimens infected with Mermithidae to be sluggish.

Observations made during 1914 seemed to indicate that the infection was confined to the females and that the parasites prevented the development of the ova. No attention was paid to the sexes of the hosts during the early part of the season, but during October only females were found to be infected.

During the infection experiments in 1916 it became evident that males as well as females became infected, and later when hosts were collected in the field for examination males were found to be almost as heavily infected as females. Of 711 males examined 64 or 9 per cent were infected and of 440 females examined 59 or 14 per cent were infected. Of the infected females many had eggs, but usually the number of eggs was smaller than in normal females, and in heavy infections with older worms there were usually no eggs present. In males no effect on the reproductive organs was noted, perhaps mainly because it is more difficult to detect a diminution of the testes than of the ovaries.

The records of 1914 showing no infection in males remained a puzzle until a collection was made on October 14. Of 10 males collected not one was infected, while in 11 females seven were infected. It is probable, then,

that the earlier collections of 1914 did not show the difference in infection between males and females that was noticed later. Whether the later difference is due to the fact that infected males die early or to the fact that males mature and lose their parasites earlier than do the females has not been determined.

No actual observations on the length of the parasitic period have been made, and since the data bearing on this subject are given elsewhere, this topic may be left for later discussion.

The period during which parasites become mature and emerge from their hosts lasts from early September until late October. In 1914 no collections were made before September 21 and only a few hosts were collected before September 23. On the latter date 78 hosts were collected and several parasites escaped before the collection was brought to the laboratory. The first large collection in 1916 was made on September 5 and yielded 64 parasites of which three were developing the brown color. Of 8 parasites obtained on September 6 one was developing color, 20 obtained September 7 were all white, but 80 collected September 8 included 5 adults ready to emerge. The other limit to the time for emergence is set by the death of the last host. In 1914 the last big collection containing 126 hosts, was made on October 3 and yielded 17 parasites. The record contains a note stating that one of the specimens was the youngest obtained to that time and that the material should be good for study as it contained specimens of all ages. After that *Orchelimum vulgare* became more and more scarce. On October 17, 54 hosts were collected and were found to contain mostly mature parasites, but a few that were not fully developed. In three further collections made respectively on October 24, 29, and 31, only that of October 29 contained a single female of *Orchelimum vulgare*. In 1916 the latest collection was made on October 14 and according to the records one parasite was still quite young. At that time the hosts were so extremely scarce that no further collections were made.

Without exception I have found the parasites escaping with the anterior end first from a region near the anus of the host. In all I have seen more than two dozen specimens of *Gordius robustus* escape from their hosts.

The mature parasites in the hosts react definitely and quickly to water. On September 24, 1914 one specimen of *Orchelimum vulgare* when caught was found to have the anterior end of a *Gordius* protruded at its posterior end. When the host was dropped into the bottle and thus the pressure on the abdomen released the parasite withdrew. After a short time the bottle was partly filled with water and the parasite emerged within one minute. On the same date two other hosts with parasites in the same stage were collected and placed in a dry bottle. During the remainder of the trip which lasted about two more hours the parasites remained in the hosts. In the laboratory the hosts were placed in water and in about one minute the

parasites, two from one host and one from the other, had escaped. On October 19, 1914, a specimen of *Orchelimum vulgare* which had been collected on October 15 and kept in a cage in the meantime, was placed in water. Within less than five minutes six specimens of *Gordius robustus* escaped. Similar observations were made several times after that. These observations show that *Gordius robustus* may remain for a long time in the body of the host after the adult state has been reached and that it escapes only under favorable conditions.

#### ORGANOGENY

On account of the large amount of material available, including specimens of nearly all ages, it has been possible to follow out the essential changes that take place from the time the larva enters the host to the time the adult emerges. The following discussion is not in any sense to be the final word on the organogeny of *Gordius robustus*, but on account of the size of the field to be covered it seems best to present at this time a general account of the changes involved and to leave certain particulars for further study by means of special methods.

#### *Metamorphosis*

The changes that take place soon after the larva has entered its host, as development is initiated, hardly justify the name of metamorphosis. There is no encystment, the larva remaining active even a short time after development has begun. The evidence for this has already been given in the discussion of the infection experiments. Growth begins at about the same time in all of the tissues of the body and parts of the proboscis (Figs. 9, 11, 15, 50-53). Development in the proboscis is at first slower than in the body, but later the difference disappears and it is impossible to locate the division between body and proboscis except from the location of the partition that exists between the two in the larva (compare Figs. 15 and 67). The parts of the proboscis that do not enter into later development are the cuticula bearing the hooks and stylets with the underlying hypoderm, the muscles, and the column of cells connecting the stylets with the partition between body and proboscis (Figs. 57, 67). The cells found in the larva at the anterior end of the intestine (Fig. 20), increase very rapidly in size at first (Figs. 11, and 15, ) but later are frequently found to have disintegrated (Figs. 67, 68, 73) and are probably to be regarded as a special organ of the early developmental stages and possibly also of the larva.

#### *Derivation of tissues*

Most of the tissues are already outlined in the larva and merely undergo further development in the parasitic stage.

*Ectodermal derivatives.* The derivatives of the ectoderm of the embryo are the cuticula, hypoderm and nervous system.

The larval cuticula is retained.



The hypoderm is derived directly from that of the larva. In the larva it is a very thin layer lying immediately beneath the cuticula and having only very few nuclei except in the rudiment of the nerve cord (Figs. 21, 49). Figures 14 and 20 are somewhat misleading in this respect as it was impossible to determine the division line between the hypoderm and the underlying muscles. Even in the young parasitic forms the hypoderm is still comparatively thin (Figs. 15, 51, 65, 66).

The nerve cord arises as a thickening in the hypoderm (Figs. 15, 55, 58) along the ventral side as indicated by the two rows of nuclei in the larva (Figs. 14, 20, 56) and may therefore be regarded as derived directly from the nerve rudiments of the latter.

The derivation of the brain is more difficult to trace and an exact determination will have to be postponed until the larva can be studied more thoroly. It arises in the posterior end of the proboscis rather late in development. In the five day parasite (Figs. 50-53) and also in the six day form (Fig. 11) its location is not yet definitely indicated. In the nine day form (Fig. 15) it is indicated by a slight enlargement of a ring of cells around the proboscis just in front of the division between the proboscis and body. In the 12 day stage the cells have become enormously enlarged, are located just outside of the muscle strands of the larval proboscis (Fig. 57) and remain connected with the hypoderm only at the extreme anterior end and on the ventral side (Figs. 67-69).

*Entodermal derivatives.* The young larval parasite possesses no entodermal derivative except the intestine and this develops directly from that of the larva. Its development is at first very rapid, so that in the five and six day stages (Figs. 11, 50-52) it makes up a large part of the bulk of the parasite and even in the nine and twelve day stages (Figs. 15, 66) it is relatively enormous.

*Mesodermal derivatives.* On account of the minuteness of all the cells and the indefinite staining reactions it has been impossible to connect the mesodermal derivatives definitely with larval structures. It is possible, however, to outline their appearance in the early parasitic stages.

In the five and seven day stages the muscles appear as minute cells between the intestine and the hypoderm (Figs. 50, 51, 54). In the nine day stage they are clearly outlined as a continuous layer of elongated cells lying just inside of the hypoderm (Fig. 55).

Since the parenchyma appears very late its origin will be taken up in the discussion of the later development.

The reproductive organs appear in the five day stage as a double row of cells on each side of the intestine, slightly dorsal in position, along the main part of the body (Figs. 50, 51). In the nine day stage (Fig. 55) and more clearly in the twelve day stage (Fig. 66) they appear as two definite ridges, just inside of the muscle layer, dorso-lateral to the intestine, and extend almost the entire length of the body.

*Later development*

From the nine day stage (Fig. 15) the parasite passes over into a spiral form and this soon straightens out into a loose spiral and finally a straight, cylindrical form with rounded ends. The straight form is often reached in twelve days. After that the parasites, tho usually coiled in the body of the host, are straight when relaxed in salt solution. In this they differ from parasitic Mermithidae which when relaxed, take the form of a helix. To the 28 day stage and beyond, the parasites are so transparent that it requires a dark background to see them. Later stages are white until the adult color develops.

Development takes place uniformly thruout the length of the body. This is shown in the stage of development of the nerve cord in figurers 29 and 72, taken from the middle and posterior end of the same specimen and in the development of the cuticula in figures 108 and 107 taken respectively from the anterior end and posterior end of a male in which the fibrous layer of the adult cuticula was in the process of formation.

In the following discussions the different tissues and organs will be taken up separately and their development traced to the adult structure. Comparisons with the results obtained by other authors will be taken up in a separate division of this report after the description of the different structures has been completed.

*Cuticula.* Earlier stages are covered only by the larval cuticula since the adult cuticula appears very late in development.

*Larval cuticula.* With the initiation of development there comes a decided increase in the permeability of the cuticula. While it is almost impossible to dehydrate and mount free living larvae without having them collapse, the early parasitic stages may be mounted with comparative ease. Together with this increase in the permeability comes an increase in the thickness of the cuticula. While in the larva and the very young form it appears only as a very fine line when magnified 800 times, in the twelve day stage it appears as a much heavier line at a magnification of only 500 times. Actual measurements give values of about  $0.35\mu$  for the larva,  $0.55\mu$  for the five day stage, and  $0.7\mu$  for the twelve day stage. This increase in thickness continues at about the same rate until the time the nerve cord separates from the hypoderm and growth has already taken place in part of the germ cells. At that time the diameter is nearly two micra. Soon after that there appears directly beneath the cuticula a finely granular layer, stainable with iron hematoxylin and alkaline methylene blue. There now appears between the larval cuticula and the granular layer a more homogeneous layer (Figs. 85, 112) not stainable in iron hematoxylin (Figs. 108, 117) but heavily stained by aniline blue in Mallory's connective tissue stain. The larval cuticula remains connected with the granular layer by very fine strands (Figs. 38). At times there appear in this layer larger

amorphous bodies which are probably due to the action of the killing agent. This homogeneous layer, as it may be called, attains a diameter of about  $10\mu$  at the time the tissues of the parasite have reached their full development and then begins to disintegrate. By the disintegration of this layer the larval cuticula becomes loosened from the underlying granular layer (Fig. 39), soon becomes torn, and is sloughed off from the body of the parasite when it is ready to leave the host. When fully developed parasites are taken from their hosts pieces of the larval cuticula are often seen trailing from one or both ends like transparent threads. The larval proboscis which has been lying just beneath the larval cuticula (Fig. 73) is also shed at this time. In some cases the deeper part of the intervening layer does not become disintegrated by the time the larval cuticula is shed and remains for a short time attached to the granular layer, but ultimately it becomes entirely removed. The structure of the larval cuticula is homogeneous thruout.

Adult cuticula. The earliest beginning of the adult cuticula is the formation of the granular layer under the larval cuticula as described in the previous section. This granular layer, which increases somewhat in thickness, but never has any very definite boundaries, forms the layer known as the homogeneous cuticula of the adult. The granules become crowded closer together so that they are not easily distinguishable.

The fibrous cuticula of the adult appears as a differentiation of the cytoplasm of the hypoderm some time after the formation of the granular layer, when the intervening homogeneous layer has already reached nearly half its final diameter (Figs. 112, 41, 35, 116). Thruout development the fibrous cuticula consists of fibrous strands connecting the granular layer with the hypoderm and of an intervening matrix (Fig. 43, 119). The intervening matrix is under the most favorable conditions resolvable into layers of fibers perpendicular to the radiating strands and forming nodules at the intersections with those strands (Fig. 43). The fibers composing these layers in the matrix are the rudiments of the ultimate diagonally intersecting fibers of the adult cuticula. The nodules at first appear to produce a thickening of the radiating fibers but later fuse along the diagonal fibers and separate from each other along the radiating fibers to form the heavy fibers of the adult cuticula. The layers of diagonal fibers are not formed in a regularly alternating series, but two layers in one direction alternate with one in the other (Fig. 38). This fact can be determined only on diagonal sections made parallel to the fibers of one of the layers. The number of layers of intersecting fibers is variable, but near the middle of the body it is about 45 (Fig. 38) and even on the prongs of the fork of the male it is seldom less than 30 (Figs. 121-123). Since in two adjacent layers of parallel fibers the fibers of one are of the same diameter as those of the alternating layer, but those of the other are much

thinner, low magnification shows the two adjacent layers of heavy fibers as a single dark layer and between two such dark layers the thinner fibers as a lighter layer, thus giving the cuticula the appearance of being composed of ten to fifteen dark layers (Fig. 124).

The adult cuticula, macerated in nitric acid and separated into thin layers, shows clearly under low magnification the rhomboids formed by the intersection of the coarser lines (Fig. 5) and under high magnification the finer intersecting fibers (Fig. 4). The coarser lines enclosing the rhomboids are due to a slight increase in the thickness of the fibers as well as in the pigmentation.

The bristles of the adult cuticula, when they first become evident, are heavy radiating strands connecting the larval cuticula with the hypoderm (Figs. 38, 40). At first they are thick and translucent, but later they become shrunken and opaque, and it is impossible to trace them beneath the first layer of the fibrous cuticula. At the time of moulting they become detached from the larval cuticula and remain attached to the surface of the adult cuticula. The bristles pass thru the granular layer (Fig. 44) and consequently are not covered by the homogeneous cuticula of the adult.

The postcloacal ridge of the male is formed by elongated cells in the hypoderm (Figs. 37, 60, 61) and appears as a thickening in the granular layer. In the adult it appears to be continuous with the homogeneous cuticula and on cross section has the appearance of a stout hook set upon a projecting base of the fibrous cuticula and curved slightly backward and inward (Fig. 98).

Over the anterior end the fibrous cuticula develops in the normal way, but is not so thick as elsewhere. Later the fibres become more closely packed together, all granular substances disappear, and the cuticula under the white area becomes nearly homogeneous and transparent.

During the entire period of development the layers of the cuticula are pure white. Pigmentation begins when the homogeneous layer underlying the larval cuticula has already begun to disintegrate. Pigmentation begins first in the dark ring behind the anterior white area. It next delineates the dorsal and ventral bands, beginning at the anterior end and passing backward. By the time these bands are shown on about the anterior fourth of the body, pigmentation of the rest of the cuticula begins at the anterior end and slightly later also at the posterior end. At this end also the dark bands appear first, but are never so clearly outlined as at the anterior end. The bands from the two ends soon come together slightly posterior to the middle of the body and the pigmentation of the rest of the cuticula proceeds in the same order. In case of all specimens observed leaving their hosts the pigmentation could not be distinguished from that of free living specimens. If specimens in which the pigmentation is not complete are

removed from their hosts the intensity of the pigmentation does not appreciably increase in the free state. Several such specimens were observed for short periods and one female with little pigmentation except the dark ring and bands was removed from the host on September 6, 1916, and kept alive in an aquarium until the beginning of March, 1917, with no appreciable increase in pigmentation. The specimen at that time died from an attack of fungus.

*Hypoderm.* In the specimens five day old the hypoderm is already clearly distinguishable as a layer of flattened cells, slightly thickened in the region of the nerve cord, and lying just beneath the cuticula (Figs. 50, 51). Partly by the thickening of the layer, but chiefly by the rapid multiplication of the cells, the latter have become cuboidal when the nine day stage has been reached (Fig. 55). By a continuation of the multiplication and the increase of the thickness of the layer the cells soon come to be columnar in character. This condition is clearly shown at the ends of the specimens in the twelve day stage, and appears over the entire body at slightly later stages (Figs. 84, 86). Multiplication of the cells appears to be complete by the time growth begins in the germ cells (Fig. 86) and further development depends upon growth. In some cases there is a secondary flattening of the cells before the development of the adult cuticula is initiated (Fig. 87), but whether this secondary flattening occurs or the cells remain columnar (Fig. 99), the small, round nuclei (Figs. 71, 73) become enlarged and flattened in a direction parallel to the surface of the specimen (Figs. 42, 99). The enlargement and flattening occur by the flowing together of several chromophil centers into one nucleus, the accumulation of achromatic substance around these centers, and the development of a definite nuclear membrane surrounding both (Figs. 70, 127). The chromatic centers remain as distinct nucleoli within the larger nuclei. As the adult stage is approached the nucleoli increase in size and become more diffused so as to occupy more or less completely the entire space within the nuclear membrane. At the same time the nucleus shrinks and becomes excessively flattened, crowding together the nucleolar matter into a dense mass (Fig. 124).

Altho in cross sections of the hypoderm the cells appear to form a syncytium with the cell boundaries merely indicated here and there (Figs. 41, 73), tangential sections and preparations of separated pieces of hypoderm show distinctly the cell outlines (Figs. 127, 128). Such preparations, however, show that the cell boundaries are not complete, the cells remaining connected with each other by numerous protoplasmic strands. During the earliest stages of the formation of the fibrous cuticula there appears within the outer part of the hypoderm a system of canals surrounding the cells (Fig. 41) and, at the intersections, sending out branches to their bases.

The hypoderm is always of greater diameter at the ends of the body than in the middle. The elongated cells forming the postcloacal ridge of the male have already been mentioned. Other modifications of the hypoderm will be taken up in the next topic.

*Nervous system.* The nervous system consists of brain, ventral cord, cloacal ganglion, peripheral fibers and nerve cells located in various parts of the hypoderm.

*Central nervous system.* The very early appearance of the central nervous system has already been described. In the description of the later development each part will be taken up separately.

As stated in a previous section, the brain is outlined at first as a ring of cells in the hypoderm of the proboscis. It soon separates from the hypoderm, remaining connected with it only at the anterior end and the ventral side (Figs. 57, 67–69). It consists at this time of a few large cells situated just in front of the partition between the region developed from the larval proboscis and that developed from the body of the larva. The cells completely surround the larval muscles and the strand that connects the stillets with the partition in the larva. These large cells remain permanently in that position (Figs. 73, 74) while the rest of the brain develops in front and around them, most of the later cells appearing antero-ventrad to the original group. By the growth of the anterior region the larval connecting strand becomes stretched out and torn, the major part of it usually remaining in the base of the brain, while the armature of the proboscis is carried forward and pushed out of the hypoderm at the anterior end (Figs. 73, 22, 23). The strand in the base of the brain later disintegrates, leaving an open space (Fig. 74). At the time the cells have reached their full development the original group forms the postero-dorsal part of the brain (Figs. 81–83), while the other cells, mostly smaller in size, surround the rest of the brain and form a heavy mass at the ventral side continuous with the cells of the ventral cord (Figs. 73, 81–83). The central core of the brain is occupied chiefly by fibres with a few scattered cells. From the ventral cell mass a group of cells projects dorsad into the anterior part of the fibre mass and tends to become separated by intervening fibres from the underlying cells. Ventral and slightly posterior to this group of cells is a large, definitely outlined cross commissure (Fig. 74) dividing at each end into a ventral and a dorsal branch. The cells of the brain appear to be multipolar but that fact has not been definitely established.

The fibres in the brain pass in all conceivable directions, and many of them are directly continuous with those of the cord. At the anterior end under the white area and part of the dark ring the hypoderm is very much thickened, most of the cells are modified into bipolar nerve cells like those which connect the ventral cord to the hypoderm in the rest of the body, and on the ventral side these fibres pass directly over into the connecting fibres of the cord.

The ventral cord arises as a thickening in the hypoderm, as has already been shown, but later becomes separated from it, passing inward even beyond the muscle layer and remaining connected with the hypoderm only by a single row of cells (Figs. 58, 105).

The cells that later make up the nerve cord at first appear as two rows of larger cells in the hypoderm (Fig. 56) corresponding to the two rows of nuclei on the ventral side of the larva. Even in later stages these two rows of cells remain clearly distinguishable altho they crowd each other so that they come to lie alternately one behind the other and do not usually show in a single section. Between these two rows of cells and on each side of them appear very early in development three longitudinal fiber tracts (Figs. 56, 58), which are the rudiments of the three main fiber tracts of the nerve cord. Nerve cells later appear under these fibre tracts and on the two sides of them (Fig. 88), separating the tracts entirely from the rest of the hypoderm. By the growth of the cells under the median tract, that is pushed out beyond the two lateral tracts, and the division between the two rows of cells becomes nearly obliterated. The cord, after separating from the hypoderm, has in cross section the shape of a loop or fan with rounded corners, the cells forming the base and projecting far into the interior.

It has been impossible to determine the structure of the smaller cells. The larger cells, where their structure could be made out, have been found to be bipolar, giving off one fibre to the longitudinal tract and one to the dorsal border of the cord (Fig. 139). The longitudinal fibres as well as the radiating fibres stain very deeply with iron hematoxylin (Figs. 105, 106, 114) but the structures shown throw little light on the physiology of the nerve cord. The longitudinal fibres have been traced only for short distances (Fig. 102). In a number of cases fibres have been found to pass over cross-wise from one part of the cord to the other (Fig. 114). Both the radiating fibres and the crossing fibres enlarge slightly toward the periphery and end abruptly at the edge of the cord.

In later stages the connection between the nerve cord and hypoderm consists of spindle-shaped, bipolar cells placed in close succession one behind the other in a single row, with nowhere an indication of a ganglion (Fig. 45).

In the male the ventral cord separates into two branches at the posterior end, a branch passing into each prong of the fork (Fig. 98) and ultimately disappearing in the hypoderm (Fig. 36). Beginning at about the point where the connection between hypoderm and cord becomes divided and passing backward to the cloacal musculature there is an enlargement of the cord, the cloacal ganglion (Figs. 101, 102). It consists chiefly of an increase of the fibrous part of the cord and hardly deserves the name of ganglion.

In the female an enlargement of the cord occurs near the posterior end, opposite the cloacal musculature (Fig. 92), while the cord is passing into the hypoderm. This appears as an enlargement of the cellular part of

the cord with fibres passing into the musculature and the hypoderm surrounding the cloacal aperture.

**Peripheral nervous system.** The ordinary methods of technic show very little of the peripheral nervous system and consequently it will have to be dismissed at this time with a few passing remarks. In a few adults stained with iron hematoxylin nerve fibres were shown passing from the nerve cord into the hypoderm and could also be traced for some distance in the hypoderm (Figs. 115, 118, 120). The fibres pass directly into the hypoderm and, some distance from the cord, are seen to lie well within the hypoderm mesad from the nuclei. At the time of the formation of the cuticula it is usually possible to detect flask-shaped cells in the inner part of the hypoderm (Figs. 42, 129) and in a few cases fibres passing outward from these cells or parallel to the surface of the hypoderm.

**Digestive system.** The digestive system consists only of a straight tube beginning near the anterior end and opening at the posterior end. Neither mouth nor esophagus is present in this species at any stage of development. The structures that might be mistaken for mouth and esophagus have already, in the discussion of the brain, been shown to be merely the spaces previously occupied by parts of the larval proboscis.

As in the larva (Fig. 20) so in the young parasitic forms, the anterior part of the intestine consists of a solid mass of cells (Figs. 11, 15), and the lumen begins behind this cell mass. Later this cell mass disintegrates, as is shown in some specimens of the twelve day stage (Figs. 67, 68). By the time the twenty-eight day stage has been reached the space left by the disintegration of those cells has been filled by mesenchyme, thus the brain and intestine have become distinctly separated and the lumen of the intestine is closed by a single layer of cells. In some cases, however, the mass of cells does not disintegrate completely until a much later stage is reached (Fig. 73). In either case the mesenchyme cells soon invade the region between the intestine and the brain, so that in the later stages the two come to be separated by a solid mass of parenchyma equal in length to more than half the diameter of the body (Fig. 74).

Whether or not there is in the larva and young parasite an outlet of the cell mass thru the proboscis, can not be determined from the material at hand. A tube can be traced from the anterior end to the base of the stylets (Fig. 47) and in some cases appears to be indicated in the connecting strand behind the stylets, but on account of the extreme minuteness of the structures as compared with the thickness of the sections it is impossible to make a definite determination. But, even if there is a tube leading from the end of the stylets to the cell mass, it never passes thru the cell mass to the lumen of the intestine.

From the early stages until the adult cuticula has been nearly completed the walls of the intestine consist of a syncytium of heavy cells with large



nuclei and with the cell boundaries only very faintly indicated (Figs. 50, 72, 73, 75, 79, 84, 86, 106). Around the outside of the intestine is a heavy membrane (Fig. 77), easily demonstrated when stained with Mallory's connective tissue stain. The inner edge of the wall is frequently differentiated into a loose, porous or spongy structure, with no definite membrane on the inner surface (Fig. 106). During the early part of the formation of the fibrous cuticula the cells of the intestine begin to decrease in size, in the adults they are excessively shrunk, and by the time the reproductive products have been discharged there is little left but the skeletal structure of the cells (Fig. 46).

At the posterior end the intestine in the very young forms opens slightly ventral (Figs. 11, 15), but by the twelve day stage has become nearly terminal (Figs. 63, 64). At that stage diverticula are formed at the points where the seminal receptacle and oviducts in the female and the sperm ducts in the male later enter the cloaca (Figs. 64, 65). The part of the intestine behind these diverticula is in the young stages lined by a heavy membrane and in the adult condition lined by the homogeneous cuticula (Fig. 78) and must be regarded as consisting of invaginated hypoderm. In the female the opening of the intestine remains terminal, but in the male it is again shifted to the ventral side. The lobes of the fork first grow out beyond the cloacal aperture (Fig. 59) and then by an overgrowth of the dorsal wall the aperture is turned to the ventral side (Figs. 60, 61). The larval cuticula does not enter the space between the prongs, but leaves this space to be filled out by a substance similar to the homogeneous intermediate layer, the intestine opening terminally thru a passage in this substance (Figs. 36, 60).

*Excretory system.* At no stage in the development is there present any trace of an excretory system corresponding in any way to the excretory systems found in other animals.

*Circulatory system.* There exists no definite circulatory system, but there are present at all stages in development spaces in different parts of the body that undoubtedly aid in the distribution of the body fluids. Very early the intestine becomes surrounded by an open space, remaining attached to the other tissue only on the ventral side. This space is later invaded to a great extent by the parenchyma but is seldom entirely eliminated. It is the only space that is usually present. In the females a second space later appears on the dorsal side between the points of attachment of the ovaries. These spaces usually do not approach the ends of the body which are filled with parenchyma.

*Muscles.* In the very young forms the muscles appear as a layer of longitudinally arranged, spindle-shaped cells, lining the hypoderm (Fig. 67). The cells are at first rounded in cross section but soon become flattened by crowding against each other so that they appear as columnar

cells in cross section with the nucleus lying close to the inner edge. As development goes on the cells become more and more flattened and elongated (Figs. 112, 117). When viewed from the edge the cells take on the appearance of very much elongated spindles with the two ends running out into fine points. From the side they appear as long blades with one edge straight and the other rounded at the ends (Fig. 126). When in position the blades are placed with the straight edge against the hypoderm and the nucleus is located in the middle of the opposite edge. The ends can easily be detected in cross section lying in the outer half of the muscle layer (Fig. 112). The nucleus, at first nearly round, later comes to be a very much elongated, flattened, oval body, lying either at the inner edge or near the inner edge of the cell, and occupying nearly the whole diameter of the cell at that point (Fig. 107).

The cytoplasm of the cell at first does not appear different from that of other cells but later there is formed a deeply staining granular substance extending from the nucleus to the outer edge of the cell; this substance finally forms longitudinal fibrils which arrange themselves in a continuous layer around the inner, spongy cytoplasm and the nucleus (Figs. 43, 105, 112, 124, 126). The fibrils are not of homogeneous structure, but are composed of serially arranged granules.

The cells at first are contiguous, but at the time the heavy walls appear in the parenchyma a substance having the same appearance and staining reactions as those walls surrounds each cell, so that the cells become separated from each other, from the hypoderm and from the parenchyma (Fig. 116). At the ends of the body the muscles gradually lose their characteristic structure and pass over into the parenchyma.

At the time of the discharge of the reproductive products the muscles begin to disintegrate slowly from the inner edge. In some specimens sectioned this process had consumed nearly the whole muscle cells (Figs. 46, 124).

The cloacal musculature of the male consists of radiating fibres around the cloaca and circular fibres surrounding the sperm ducts just before they enter the cloaca (Figs. 96, 97). In the early stages the cells are not differentiated from parenchyma cells, but later they become very much elongated and in the adults lack the heavy cell walls that are found in the parenchyma. The radiating fibers arise from the dorsal and lateral walls of the cloaca and extend for the main part in a dorso-lateral direction.

The cloacal musculature of the female consists of a heavy circular muscle forming the constriction between the cloaca and the sperm receptacle (Fig. 94) and weaker circular muscles around the oviducts. The fibers are similar to those of the male cloacal musculature. There is also present a heavy group of circular fibers around the posterior end of the cloaca, and a sheet of longitudinal fibers surrounding the glandular part of the

cloaca. These fibers are intermediate in structure between muscle fibers and parenchyma cells. They are elongated, closely compact, but do not stain as deeply as muscle cells and possess walls nearly as heavy as those of the parenchyma.

*Parenchyma and mesenteries.* The parenchyma arises first as spindle-shaped or multipolar mesenchyme cells (Figs. 63, 67-69). Most of the cells appear to arise at the ends of the body, but a few cells are also found in the intermediate region at a very early stage and may arise there. In the twelve day stage many of the cells are not distinguishable from muscle cells between which they are frequently inserted, and even in much later stages the distinction between the two kinds of cells is not always clear. The cells remain generalized for a long time and are scarcely distinguishable from cells that form the rudiments of other organs (Fig. 109).

The multiplication of the cells takes place very rapidly. In the male they often fill completely the spaces between the organs. Except at the ends, where they form a solid mass from the beginning, they first form an irregular layer lining the muscles and the nerve cord and forming triradiate septa which enclose the germ cells. Ventral to the germ cells the cavity still remains and the intestine is attached to the layer of cells over the nerve cord (Fig. 75). By further multiplication of the cells the germ cells become farther removed from the muscles and all or nearly all of the space becomes invaded (Figs. 107, 108).

In the females the multiplication of the cells is not so prolific. The layer lining the muscles and nerve cord and holding the intestine in place is formed as in the males, but it passes between the muscles and the ovaries only at the end of the body, leaving the ovaries in contact with the muscles thruout nearly their whole length. A few mesenchyma cells enter between the ovaries and others are scattered thruout the body at different places, but there are no definite layers enclosing the germ cells (Figs. 76, 79, 86). By the later growth of the eggs nearly all of the spaces in the body are eliminated.

A short time before the adult cuticula is formed the cells become surrounded by heavy layers of a hyaline substance that is stained with aniline blue in Mallory's connective tissue stain. The cells then lie in cuboidal, rounded, or polygonal chambers completely isolated from each other (Figs. 112, 116). Very soon the cells become shriveled, leaving only the heavy walls with here and there a fragment of a nucleus or of cytoplasm.

The layer of parenchyma immediately surrounding the nerve cord deserves special mention on account of its peculiar mode of development. In early stages, when the nerve cord is merely a thickening in the hypoderm, this layer is continuous with the muscle layer lining the rest of the hypoderm and can at first not be distinguished from that layer (Fig. 84). Even when fully developed these parenchyma cells are narrow and very much

elongated and in that respect resemble muscle cells (Fig. 102). These cells are themselves covered by the layer of mesenchyme cells that later lines the muscles. Ultimately, however, there is no difference between the prechyma cells that originally covered the nerve cord and those that later migrated over them, the one passing gradually into the other (Fig. 106).

At times the intestine becomes separated from the underlying layer and remains attached to it by a longitudinal sheet of cells of single thickness, the ventral mesentery. The intestine adheres to a broadened surface of the terminal cell, but its outer membrane is in no way continuous with the covering of that cell. The structures by which the egg masses appear to be suspended in the older females are not mesenteries but the remains of the ovaries and will be discussed in the next section.

*Reproductive organs.* In the early stages one can find no difference between males and females. The first difference appears in the character of the diverticula formed at the posterior end of the intestine. In the female three diverticula are formed (Fig. 109), one for the seminal receptacle and two for the oviducts, while in the male only two appear for the sperm ducts (Fig. 29). These diverticula have made their appearance before the 28 day stage (Figs. 64, 65). Somewhat later the ovaries become differentiated from the testes by the formation of buds along the ventral sides (Figs. 76, 84, 86). These buds are not always opposite in the two ovaries nor are they of uniform size (Fig. 62).

Each ovary at first is enclosed by a definite, heavy membrane, but later the membrane becomes thin at the buds and the eggs pass into the body cavity soon after they have begun the growth period (Figs. 76, 84, 86). The eggs, however do not lie loose in the body cavity, but continue to be enclosed in thinner membranes of the ovary. By the time the first eggs have reached their full size nearly all of the germ cells have left the ovarian tubes and have in masses, strands, or sheets become distributed among the developed oocytes which tend to form layers around them. As the increase in the diameter of the body continues, the ovarian tubes become broadened dorso-ventrally, and by the discharge of the germ cells they become flattened, so that they take the form of broad, thin sheets suspended from the dorsal muscles (Fig. 79). In later stages they remain as double membranes still helping to support the masses of eggs in the body cavity. The extensions of the membranes at the buds have become thrown into many folds and have been thickened in places to help in the support of the ovarian mass. At the time of the discharge of the eggs the membranes become ruptured and the heavy parts remain attached to the dorsal muscles (Fig. 46).

The growth period in the oocytes begins somewhat before the homogeneous layer is formed under the larval cuticula and continues until the formation of the adult cuticula is well under way (Figs. 76, 86, 77). It does

not occur simultaneously in all of the germ cells but progresses from the buds toward the dorsal part of the ovary. The full-grown oocyte is about 0.023 mm. in diameter and is surrounded by a definite membrane. At the center of the cell is found a large nucleus, while the cytoplasm is filled with yolk granules. The nucleus has a diameter of about 0.006 mm. and consists of a large, central chromophil mass surrounded consecutively by an achromatic and a chromatic layer (Fig. 106).

Toward the anterior end the ovaries gradually decrease in size, the space surrounding them, even on the dorsal side, becoming filled with parenchyma. In some cases the invading parenchyma interrupts the ovaries at places, forming bead-like masses following each other in longitudinal series. The formation of these masses is even less regular than the location of the buds on the ventral sides of the ovaries.

At the posterior end the oviducts are formed by continuations of the ovaries and they unite to form the cloacal gland and the seminal receptacle (Figs. 109-11). It has been impossible in the very early stages to recognize the germ cells in this region, but at the time the ovaries are still round they pass without interruption back to the point of union and form a mass of cells, the rudiment of the cloacal gland, around the ventral side of the intestine. At that stage the lateral diverticula connect with these cells near the latero-posterior margins of the mass while the ventral diverticulum joins them somewhat anterior to those points. The seminal receptacle exists as an anterior lobe of the cell mass. The membrane surrounding those structures is continuous with those surrounding the ovaries and no difference is apparent in the character of the cells of the cloacal structures and the ovaries, either in staining reaction or in structure.

Later the cells become modified so that it is impossible to distinguish between those that have been derived from the intestine and those derived from the germ glands. The oviducts become indistinguishable behind the points where they enter the cloacal gland. Anterior to those points the cells in the oviducts rearrange themselves so as to form definite walls around the central ducts (Figs. 88-90, 93-95). Even at that stage the change from oviducts to ovaries is a gradual one, the oviducal walls continuing farther anterior on the ventral side than on the dorsal.

The cloacal gland takes up a median position beginning somewhat posterior to the points at which the ovaries were previously inserted into the intestine and extending anterior to the seminal receptacle, into which it opens broadly (Figs. 78, 93-95, 99, 100). The intestine opens into the dorsal side of the gland near its posterior end, the oviducts open into the latero-ventral sides near the anterior end. The cells of the gland become closely packed and form finger-like projections that extend inward and forward

into the seminal receptacle. The large muscle surrounding the posterior part of the gland has been described under the topic of cloacal musculature.

The seminal receptacle extends forward as an elongated sac with definite walls similar to those of the oviducts at their posterior ends. It is empty and distended, occupying in cross section fully one half the diameter of the body and extending lengthwise over a space equal to three or four times that diameter. The intestine passes around to the ventral side of the body before the end of the seminal receptacle has been reached.

The testes in the males remain as cylindrical or somewhat triangular tubes extending nearly the whole length of the body (Figs. 72, 80, 107, 108). They are enclosed in heavy membranes and very early become completely surrounded by parenchyma cells. As in the ovaries so in the testes there are never any traces of cellular walls.

At the anterior end the testes are subject to bead formation similar to that in the ovaries. The sperm ducts are posterior extensions of the testes, opening into the intestine a short distance anterior to the anus, and in the early stages in no way distinguishable from the testes (Figs. 29, 70-71). Cellular walls for the sperm ducts are formed only within the cloacal musculature, anterior to that all of the cells develop into spermatozoa. The intestinal diverticula as in the case of the females consist of nothing more than a turning out of the walls of the intestine at those points.

The transformation from spermatocytes to spermatozoa begins at a slightly later stage in development than does the growth of the oocytes in the female. It takes place almost simultaneously in all parts of the testes and is completed before the adult cuticula has been fully formed.

The chromatin rod appears as a semicircle at one side of a rounded cell, but later becomes straightened and takes up a median position while the cell becomes spindle-shaped. At the same time the cytoplasmic contents pass to one end leaving the rod at the other end surrounded by only a thin layer of cytoplasm, the thickest part of the spindle being either at or even beyond the end of the rod (Figs. 12, 13, 18, 19). In this form the spermatozoa leave the male. Before they pass into the body of the female they become somewhat elongated (Fig. 10). In the seminal receptacle of the female the cytoplasmic part of the spermatozoon elongates into a heavy flagellum of uniform diameter while the rod remains as a slightly thickened head at one end (Fig. 17).

## OBSERVATIONS ON PARAGORDIUS VARIUS

On account of the excellent description of the adult organization of this species by Montgomery in 1903 and on account of the general similarity in the development of this species and the one just described, the following description will be made as brief as possible.

### DETERMINATION OF THE SPECIES

Nothing needs to be added to the descriptions of this species given by Montgomery (1898, 1903) except that here also, as in *Gordius robustus*, there are present two longitudinal, darker bands; a broader dorsal and a narrower ventral band. They are even more distinct than in the previous species.

### HABITS OF THE ADULTS

This species prefers quiet water to rapids and more frequently inhabits lakes than streams. It is not very abundant in the waters about Urbana, but is the common species reported from the Great Lakes region. Nothing has been observed in regard to the winter habitat. The earliest specimens were taken near Urbana the latter part of May, 1914. At Douglas Lake large numbers were emerging from their hosts the latter part of June, 1915. While at Urbana both males and females were found in the grass at the water's edge, only males were found in similar positions at Douglas Lake. Females that had emerged during the night could still be found swimming near the shore, but during the entire summer of 1915 only a few females were found that had wound themselves around grass and had laid eggs.

Females that have just emerged, while swimming near the shore, soon encounter males and copulation takes place. The deposition of eggs begins the following day. On June 27, 1915, an adult female was removed from a host. It was kept alone in an aquarium until the 29th, when it was placed with a male in a large vessel and mating was observed. The next morning it was found to have laid a string of eggs. Another female removed from the host on June 30 and mated on the same day laid eggs July 1. Other similar cases were observed.

Mating was observed in several cases. The process is in every respect similar to that described for *Gordius robustus*. The male more actively responds to the stimulus from the female and the discharge of sperm is almost instantaneous. There is again no choice of direction and discharges of sperm may in some cases take place at other parts of the body of the female than the posterior end. There is no interlocking of the lobes at the posterior ends of the two specimens, and after copulation the spermatozoa

remain in a large mass enveloping the lobes of the female, but pass into the seminal receptacle in less than a day.

On July 9 a mutilated male was obtained from the lake. It consisted of the posterior end of the body with more than a third of the body removed from the other end. A female was placed with this male and after a few hours showed a m.v. of spermatozoa at the posterior end.

The eggs are deposited in long strings about 0.2 mm. in diameter, and adhere very tenaciously to each other. Females will deposit eggs in aquaria just as freely as in nature. When grass or other objects are present the strings are wound around them, otherwise they are deposited in large, tangled masses.

Males and females that have discharged their reproductive products die and disintegrate in the manner described for the previous species.

#### EARLY DEVELOPMENT

The observations made on the development and structure of the larva are, for reasons stated before, only fragmentary and can not be included in this report.

#### PARASITISM

Like *Gordius robustus*, this species enters a host as larva and undergoes its entire development in the parasitic stage.

*Hosts.* Both at Douglas Lake and Urbana parasitic stages were found in adults or older nymphs of *Gryllus assimilis* (Fabricius) as defined by Rahn and Hebard (1915). At Douglas Lake they were also found in *Nemobius fasciatus* (DeGeer). The specimen taken from *Nemobius* were as a rule smaller and shorter in proportion to their diameters than were those taken from *Gryllus*.

Altho the larvae penetrate the tissues of various species of aquatic animals it has been impossible to determine if any or all of these animals may serve as intermediate hosts. If some of them do serve as intermediate hosts they must serve merely as carriers. The delicate tissues that appear as soon as the larva begins to change into the parasitic form make it impossible for a further change of hosts to take place without causing the destruction of the parasite. Attempts to infect the hosts artificially proved unsuccessful.

*Infection.* Only two infected hosts were taken at Urbana. At Douglas Lake in 1915 adults were emerging from the hosts in large numbers the latter part of June and young parasitic stages were still found by the middle of August. Early parasitic stages were obtained thruout the entire summer.

Infection in this species also was extremely local and slightly heavier in females than in males. Of 125 males of *Gordius assimilis* collected on the hill just above the laboratory and within half a mile of the lake 6, or 5 percent, were infected, yielding 7 parasites. Of 152 females collected at the same place 24 were infected, making an infection of about 17 per cent and



yielding 31 parasites. In collections of the same species made near the shore 154 males yielded 35 infected specimens or an infection of 23 per cent and contained 52 parasites, 276 females contained 135 infected specimens or an infection of 49 per cent and yielded 377 parasites, averaging more than two parasites to each infected host. During the latter part of the summer 37 large nymphs were collected on the hill about two miles from the lake and not a single one was found to be infected. The specimens of *Nemobius fasciatus* were all collected near the shore. Of 15 males 8 were found to be infected, yielding 16 parasites, and of 24 females only 6 were infected containing 12 parasites.

The habits of this host also make an intermediate carrier not necessary. I have several times found crickets accumulated in large numbers about pools of water at night. The fact that many unmated females of *Paragordius varius* were found in the shallow water of the lake during the early forenoon, but disappeared later, indicates that infected hosts get into the water and lose their parasites during the early morning. The local character of the infections shows that infection takes place at or near the water's edge.

*Location in the host.* Early developmental stages of *Paragordius varius* have not been found in sections of hosts. In later stages the parasites lie free in the body cavity (Fig. 134). In dissections the location in the host is found to be in every respect similar to that of *Gordius robustus*.

Practically no effect of the parasite on the host was found except in cases of very heavy infection. In those cases a diminution in the size of the reproductive organs could be detected.

*Length of parasitic period.* Since experiments were unsuccessful, no direct observations on the developmental period could be made, and since infection took place almost uniformly thruout the summer, the time of infection and time of emergence could also not be taken as criteria. The earliest appearance of adult parasites in nymphs, however, produced some valuable evidence on the subject. Most of the nymphs of *Gryllus* appeared during the last week in June and *Nemobius* did not hatch until about a week later. By the middle of August adult parasites were found in the nymphs of both species. The first adult *Paragordius varius* from *Nemobius fasciatus* was obtained on August 14 while the host was still a nymph. The developmental period can not possibly have been more than six weeks. Some of the first infected specimens of *Nemobius fasciatus* were obtained on August 2, and the parasites at that time were mostly younger than the 28 day stage in *Gordius robustus*. On August 12 most of the parasites were of nearly adult size.

*Emergence* in this species occurs in a manner similar to that in *Gordius robustus*. About six specimens were seen leaving their hosts. In all cases the parasites emerged with the anterior end first from near the anus of the

host. The definite reaction toward the presence of water was again observed. On July 12 a male of *Gryllus assimilis* was found to have the anterior end of a female of *Paragordius varius* protruding from the posterior end when it was caught. The cricket was placed in a dry vial and the parasite withdrew and remained in the host until the latter was placed in water in the laboratory two hours later. In the water the parasite left the host in less than five minutes. The emergence was witnessed by Dr. W. W. Cort and Mr. A. C. Conger. Other similar cases were observed during the summer.

#### ORGANOGENY

On account of the lack of material in the early stages little can be said about the metamorphosis and derivation of tissues in this species. Only two young specimens were obtained and they were mounted as totos (Figs. 130, 131).

*Cuticula.* Stages in its development in this species are even more difficult to obtain than in *Gordius robustus* indicating that the cuticula develops with extreme rapidity.

*Larval cuticula.* It was in this species that the shedding of the larval cuticula was first observed. Nevertheless, its presence is difficult to demonstrate during the development of the adult cuticula. It is clearly evident in younger stages and changes in size and thickness during development just as does that of the previous species. But no homogeneous layer appears under it before the beginning of the development of the adult cuticula. Much later, when the fibrous cuticula has almost reached its full development, a very thin, homogeneous layer appears under the larval cuticula (Fig. 167) but is difficult to distinguish because it adheres closely and has nearly the same density and staining reactions. The larval cuticula later separates from this layer (Fig. 163) and comes off in large sheets, being retained longest at the ends. Adult specimens removed from their hosts frequently show these pieces of the larval cuticula trailing from the two ends. When such sheets of larval cuticula are mounted and stained they show a perfectly homogeneous structure.

*Adult cuticula.* The development of the adult cuticula commences with the formation of a rather indefinite granular layer under the larval cuticula, but almost simultaneously there appears under this a lighter layer which is the beginning of the fibrous cuticula. The granular layer is the rudiment of the homogeneous or non-fibrous cuticula and areolar structures of the adult. Fibrous cuticula and areolar structures develop simultaneously (Figs. 161, 169). The stains employed failed to bring out any structures in the fibrous cuticula during its development. The hypoderm cells often give off conical projections into the developing cuticula and the apices of the cones can sometimes be seen to extend to the granular layer (Figs. 166, 167). At the points where the apices reach the granular

layer the latter becomes thickened and in it are developed hyaline bodies, usually two at each point (Figs. 104, 161, 169). These hyaline bodies later become oval in outline and give the cuticula its areolated appearance (Fig. 160). The homogeneous cuticula, which always remains more or less granular, is formed from the granular layer chiefly over these bodies, but also between and under them. The connections between the granular layer and the hypoderm remain as definite protoplasmic strands, coming to the surface usually between the oval bodies (Figs. 1, 160, 164). At intervals heavier protoplasmic strands pierce the fibrous cuticula, and over them the granular layer thickens to form the short cuticular tubercles or bristles which are found especially in two ventral rows, but also sparingly scattered over the rest of the body (Figs. 140, 164). Where the heavier strands pass thru the cuticula the fibers remain separated to form a cross (Fig. 1). At the sides of the male cloacal aperture the bristles in the two ventral rows are very much elongated. Anteriad from that point they gradually shorten, posteriad they remain high to the bases of the prongs and then become shorter and are scattered over the inner ventral surfaces of the prongs (Fig. 133). The oval bodies are absent on these surfaces.

The outer surface of the homogeneous or non-fibrous cuticula is usually hyaline in appearance, while the granules remain evident in a lower layer which indefinitely grades into the hyaline layer, and at places may be absent or at others may reach the surface. The bristles are composed chiefly of the hyaline substance, but usually show at the base a cone of the granular material. Since the granular substance stains deeply it has been impossible to trace the protoplasmic strands farther than to the bases of the bristles.

Fibers do not appear in the cuticula until it has reached nearly its full diameter. They are wound spirally around the body in two directions so that they cross each other forming antero-posterior angles of about 175 degrees and lateral angles of about 65 degrees (Fig. 1). Since the fibers are all of the same size and the layers alternate regularly, cross sections of the cuticula do not present the appearance of stratification so obvious in the cuticula of *Gordius robustus* unless the sections are made nearly parallel to one set of fibres. The number of layers of fibers is variable, but seldom exceeds 24. Montgomery reports only 11, but his figures show that he made his counts on sections parallel to one series, and counted only alternate layers. Over the white surface at the anterior end the fibers become more closely packed and tend to form a homogeneous mass.

The color appears in the manner described for *Gordius robustus* and reaches its full intensity before the parasite leaves its host. On June 30 a female was removed from the host when it was still incompletely colored. The dark ring and the dorsal and ventral bands were clearly outlined.

color had begun to appear over the rest of the cuticula at the two ends, but the middle region of the body was still white. The specimen was kept alive until July 26, when it was attacked by fungi and had to be killed. It had been mated and had laid some eggs, and had been kept in an open glass dish in the window where the sun shone on it part of the day; but the color had not noticeably changed except that the white had become soiled.

*Hypoderm.* The hypoderm in this species develops very much as in *Gordius robustus*. The cells at first are flattened, very early become columnar, and after the completion of the adult cuticula become flattened again over most of the surface of the body. They remain higher at the two ends. At the anterior end, under the white surface, they project far into the interior, becoming rod-shaped or almost fibrous in nature. The nuclei remain in the outer halves of the cells while the lower parts become clear and form a distinct mass just anterior to the supraesophageal ganglion. These hyaline bases of the cells later disintegrate or else form a substance that is dissolved during the preparation of the mount (Figs. 153, 154).

Protoplasmic connections between the hypoderm cells are present in this species as in the previous one but no canal system has been found. The cells are in cross section more easily distinguishable than in *Gordius robustus*.

The nuclei from the first are more distinct than in *Gordius robustus* and each consists of a large central nucleolus surrounded by an achromatic sphere and a somewhat indefinite membrane (Figs. 165, 170). Later the membranes become more distinct, but the nuclei do not become so definitely outlined as in *Gordius robustus* and the fusion of chromatic spheres occurs only in very few instances. During the formation of the adult cuticula the chromatic substance increases in quantity and becomes scattered thruout the nucleus (Fig. 167). In the adult stage the nucleus shrinks and the chromatic substance forms one or two discs, almost completely filling the membrane.

*Nervous system* This system is built on the same fundamental principle as in the previous species, but while some parts stand out clearer, the structure of the others is not so easily brought out.

*Central nervous system.* The brain in this species also appears in the posterior part of the proboscis, but does not begin its development until even later than in *Gordius robustus*. The rudiment of the brain appears as a group of deeper staining cells around the connecting strand between the stylets and the base of the proboscis (Fig. 162) but the cells soon lose their staining properties and become indistinguishable from the mesoderm cells which surround them (Fig. 151). The bundles of nerve fibres leading from them can, however, be distinguished. Even at a much later stage, when the nerve cord is beginning to separate from the hypoderm, the ganglion cells are difficult to distinguish from the rest.

At that time the main group lies in an indefinite mass over the esophagus, just anterior to the end of the nerve cord, and is connected with the cord by two large commissures passing around the esophagus. Under the esophagus, at the very end of the cord, a smaller group of ganglion cells is more easily distinguishable.

In further development the dorsal group becomes completely isolated from other tissues, remaining connected only with the nerve cord by the commissures and in some cases also with the anterior hypoderm by scattered, half disintegrated fibres (Fig. 153). No marked change occurs in the ventral group. At the sides of this group fibres pass anteriorly to the anterior hypoderm cells. The fibres usually become more or less definitely separated into two ventral and two lateral tracts.

The ventral cord arises and develops as described for *Gordius robustus* (Figs. 135, 146, 147, 158). The cellular elements do not all remain under the fibre tracts, pushing up into them as they did in *Gordius robustus*, but grow up over the sides, partly enclosing the fibres and leaving them in contact with the parenchyma over only about one third of the circumference, in later stages even less (Fig. 141). On account of this overgrowth of the cells the cross fibres do not present a radiating appearance but cross each other at various angles within the cord. There are, however, two longitudinal rows of heavier fibres originating from the two primary cell rows and passing to the dorsal side of the cord, dividing the longitudinal fibres into three main tracts (Fig. 159).

The structure of the large cells in the two primary rows is more easily demonstrated in this species than in the previous one. The cells are bipolar, giving off one fibre to the dorsal wall of the cord and another to the longitudinal fibre tract (Fig. 139). The body of the cell is rounded or flask-shaped and the two fibres are given off at one side. Some smaller cells were also found to be bipolar and of similar structure, but in case of the majority of the smaller cells it is impossible to make out the exact structure.

No cell bodies can be distinguished in the connection between the nerve cord and hypoderm after the two have separated, but fibres can be traced thru it from the cord to the hypoderm. At the point where the fibres from the cord enter the hypoderm longitudinal fibres are frequently found, and these fibres in some cases separate to form a longitudinal canal, the sub-neural canal of European workers.

In the male the nerve cord ends at the posterior end as it does in the previous species. The cloacal ganglion consists of a slight thickening of the cord beginning somewhat anterior to the musculature of the sperm ducts and extending back to the point of bifurcation of the cord (Fig. 164). It is intimately connected with the musculature of the vasa deferentia.

The cloacal ganglion in the female is similar to that found in *Gordius robustus* but presents some modifications on account of the posterior exten-

sion of the dorsal and lateral lobes. The nerve cord ends at the beginning of the lateral lobes and is partly inturned with the hypoderm that lines the cloaca. On account of this inturning the cord passes into the hypoderm not on the external body surface as it does in *Gordius robustus*, but in the ventral wall of the cloaca. Here the longitudinal fibers pass into the hypoderm and to a less extent than in the previous species they also pass around to the dorsal side of the cloaca.

*Peripheral nervous system.* Just as in the previous species the peripheral nervous system consists of fibers and cells in the hypoderm. Since these structures were clearly described by Montgomery, no detailed account of them will be given here.

*Digestive system.* This system is like that found in *Gordius robustus*, but in the adult condition does open to the exterior at the anterior end.

*Mouth and esophagus.* In this species the strand of cells which connects the stylets to the base of the proboscis remains attached to the anterior end of the intestine and is not only retained in the tissue, but actually undergoes development. At first it is a very short connection between the part of the proboscis that does not develop and the anterior end of the intestine, but as development proceeds it elongates and thickens, forming a bulb-like enlargement in front of the intestine with an elongation projecting dorsally over the end of the latter (Figs. 151, 153-4). It passes thru between the dorsal and ventral cell groups of the cephalic ganglion and between the two commissures. In the young stages it has been impossible to demonstrate definitely the presence of a tube in this strand. Altho some sections give the appearance of the presence of a capillary tube, this tube, if present, is so small and its walls so indefinite that it cannot be traced. At about the time the adult cuticula is formed most of the cells composing the strand disintegrate, forming a tube about which the parenchyma cells form fairly definite walls. Some of the outer cells of the strand usually also remain intact and take part in the formation of the walls (Figs. 153-4). By the loss of the proboscis, when the larval cuticula is shed, the tube is opened at its anterior end.

*Intestine.* The development of the intestine proceeds in this species much as it does in *Gordius robustus*. Here also diverticula are formed to receive the oviducts and sperm ducts (Figs. 148, 165). The cells of the intestinal walls are more easily distinguished than they were in the previous species, and an inner, vascular zone is never differentiated. The modifications at the posterior end will be taken up in the discussion of the reproductive system.

*Excretory system.* This species also presents no trace of an excretory system

*Circulatory system.* No vessels are present, but longitudinal cavities are present in this species as they were in *Gordius robustus*. Here also the main

cavity lies around the dorsal part of the intestine and may be divided by the gonads into a median canal over the intestine and two lateral canals, or the median canal may be absent (Figs. 145, 158). In the males frequently the parenchyma fills the entire space, leaving no cavities around the intestine. In the females there is usually also a cavity on the dorsal side between the ovaries. This is seldom present in the males. In later stages, when part or all of the reproductive products have been discharged, other cavities appear in both males and females.

*Muscles.* As in the previous species, these consist of a cylinder of longitudinal fibers just beneath the hypoderm and of the cloacal musculatures. The cylinder of longitudinal muscles is interrupted only on the ventral side by the connection between the nerve cord and the hypoderm, and is lost in the parenchyma before the extreme ends of the body are reached.

*Longitudinal muscles.* The longitudinal muscles begin their differentiation slightly later than they do in *Gordius robustus*. In the youngest specimens sectioned they are still similar to mesenchyma cells, and appear rounded or cuboidal in cross section, but have the shape of short spindles when viewed from the side (Figs. 147, 155, 156, 165). Later the ends elongate, and the main bodies of the cells become crowded inward by the intercalation of the elongating ends near the hypoderm. Soon, however, the bodies of the cells also elongate and the diameters become nearly equal at the inner and the outer edges. The ultimate shape of the muscle cell is essentially the same as in the previous species, but the cell is even more elongated and the nucleus is very much elongated so that it extends even into the narrower parts of the cell (Figs. 6, 158, 174). The adult muscle cell shows a layer of longitudinal fibrils, similar to that of the previous species, lying just inside the cell membrane and completely surrounding the remainder of the cell. Some of the cells that are crowded inward by the nerve cord and come to lie at the side of the connecting lamella develop into muscle cells, so that some of the muscles appear to be inserted on the lamella.

*Cloacal musculature.* The radiating cloacal musculature of the male, so prominent in the previous species, is lacking in *Paragordius varius* except for a few longitudinal fibres at the posterior side of the cloaca which are clearly continuous with the longitudinal body muscles.

The circular muscles around the sperm ducts are located a short distance anterior to the cloaca and are more highly developed than in the previous species (Fig. 164). They develop from mesenchyme cells (Fig. 142).

As in the female of *Gordius robustus*, so in the female of *Paragordius varius*, circular fibers are found chiefly around the duct connecting the cloacal gland with the seminal receptacle, but also surrounding the gland itself and in a thin sheet even surrounding the cloaca behind the gland. Very thin layers of these fibers also surround the oviducts. The fibers develop

from mesenchyme and in the later stages have heavy walls similar to those of the parenchyma.

*Parenchyma and mesenteries.* The parenchyma arises as in the preceding species, but fills the body cavity more completely in the early stages. It not only forms the lining for the muscles and surrounds the testes in the males, but it also surrounds the ovaries in the females. As the ventral buds in the ovaries appear and the eggs fill the body cavity, the inner walls of the ovaries become extended around the intestine to the sides of the nerve cord, and in that way the two mesenteries are formed (Fig. 158). The outer walls of the ovaries are turned back upon themselves at the points where the buds arise, and thus double lamellae are established reaching from those points to the muscles on the dorsal side of the body. There the layer of each lamella that lies next to the original ovarian tube is continuous over that tube with its inner wall, while the outer layer of the lamella is continuous with the outer covering of the ovarian bud, passing close to the lining of the muscles, around to the ventral side to join the ventral edge of the mesentery, or inner wall of the bud. As development proceeds, the germ cells leave the primary ovarian tubes, just as they do in *Gordius robustus*, and the outer walls of these tubes appear as parts of the mesenteries. As a result the mesenteries in later stages appear to be composed of three layers of cells in the dorsal part of the body, but of a single layer in the ventral part (Fig. 159). Even in the males the parenchyma forms about the gonads more definite layers than were found in *Gordius robustus* (Fig. 174).

During the formation of the adult cuticula heavy walls appear about the parenchyma cells, in many cases much heavier than in the previous species (Fig. 164). The cells are normally somewhat elongated, polyhedral or barrel-shaped (Figs. 3, 164), but may in other cases have the irregular polyhedral form found in *Gordius robustus*. The cells in this species remain more intact and more completely fill the spaces.

In the anterior end, behind the dorsal group of ganglion cells, the mesenchyme cells become crowded together very closely and form a capsule which encloses the ganglion cells on all sides except that covered by the flattened anterior surface (Figs. 153-4). This capsule is formed just before the heavy cell walls appear. Its adult structure has been adequately described by Montgomery.

*Reproductive organs.* The germ cells arise as in *Gordius robustus*, and in early stages can not be distinguished from mesenchyme cells in other parts of the body (Fig. 136). In the middle of the body the gonads assume a definite shape before they become surrounded by mesenchyme cells, which at that time have become easily distinguishable (Figs. 147, 156, 157). After that the mesenchyme proliferates very rapidly and completely envelopes the gonads with definite layers. The gonads of the two sexes can not be distinguished in the early stages.



Development of the testes in the male proceeds as described for *Gordius robustus*. The membranes enclosing the testes are usually not so heavy as in that species and the cellular parts of the sperm ducts extend both anterior and posterior to the short muscular areas.

The spermatozoa develop as in the previous species except that the head and cytoplasmic parts become more definitely separated before the axis of the cell becomes straightened, causing the spermatozoon to be doubled upon itself when it is first formed (Fig. 137). Head and cytoplasmic part are definitely separated from each other. In the seminal receptacle of the female the cytoplasm elongates into the heavy flagellum of uniform diameter (Fig. 138).

The reproductive organs in the female develop very much as they do in *Gordius robustus*. The membranes forming the primary ovarian tubes are not so heavy as in that species. The cloacal structures arise essentially as in *Gordius robustus*, but show modifications in certain details.

The part of the cloaca lined by the invaginated hypoderm forms a tube at the posterior end of the body equal in length to at least twenty times the diameter of the body at that point. The intestinal diverticula arise a short distance anterior to the point of union between ectoderm and entoderm and are less distinct than in *Gordius robustus*, appearing only as the points at which the intestinal wall begins to become modified. The oviducts develop from the posterior ends of the primary ovarian tubes and unite to form the rudiment of the cloacal gland and seminal receptacle. The receptaculum seminis becomes distinctly separated from the gland, remaining connected by a narrow neck (Fig. 168). The ovaries open at the sides into the anterior end of the gland and the intestine opens into it on the dorsal side at the posterior end, or perhaps it would be more correct to say in this case that the gland opens into the ventral side of the intestine. (Figs. 168, 171).

At the point of union between entoderm and ectoderm a constriction or valve appears in later stages (Fig. 171). The inner ends of the cells lining the cloaca between the valve and the cloacal gland secrete a clear substance that almost completely fills the lumen of the tube. A similar substance is secreted by the cells lining the oviducts. Radiating from the cells are thin membranes apparently enclosing the substance, and a heavier layer surrounds the remnant of the lumen. In the adult stage the inner part of the secretion is swept away and little remains except the bases of the membranes which Montgomery regarded as cilia. The hypoderm of the posterior region of the cloaca also secretes a hyaline substance which passes in long threads thru cuticular pores into the lumen (Figs. 7, 171). This substance disappears at the time of the entrance of the spermatozoa and may aid in their migration into the seminal receptacle, but the secretion of the substance continues after insemination.

The epithelium of the cloacal gland at the time of the formation of the adult cuticula develops projections in which the cells appear like buds on central stalks. (Fig. 163.)

In specimens that have deposited their eggs the cells become shriveled and the body cavity contains only the nerve cord, a very small intestine, and the parenchyma membranes, which now have all taken more or less a dorso-ventral position and tend to flatten the body in that direction (Fig. 103).

## DISCUSSION

In the following discussion I shall compare briefly the results obtained in the present investigations with those obtained by other authors and give interpretations of some of the facts observed. In the comparisons I shall confine myself almost exclusively to the more recent literature. The lack of proper methods of investigation makes the reports of the older writers of little value except as historical documents.

### BIOLOGY

Altho the behavior of the Gordiacea has attracted the attention of all workers who have obtained living material, the observations have for the most part been fragmentary and have yielded little that is of scientific value. Even the present report does not pretend to be more than the mere beginning of a systematic study of the behavior of certain species during the different stages of their life cycle.

#### *Occurrence and behavior of adults*

Various workers have reported that among the Gordiacea there is a predominance of males over females. The most recent statement to that effect was made by Meyer (1913), who reported that he collected 201 specimens and found only 6 to be females. Von Linstow (1891) found that the proportion of males to females was 7:3. More recently Mühldorf (1914) stated that in his collections, which were perhaps larger than any previous collections made, he failed to find any consistent difference in the number of males and females.

With the additional information presented in this paper it is possible to explain the previous observations and to show that the differences observed were apparent and not real.

Von Linstow gives a table of the specimens collected by him, including both free living and parasitic forms. His conclusion is based on the entire collection which included 31 females and 74 males, and does not hold true either for the free living forms or the parasitic forms when considered separately. In case of the parasitic forms he actually found three males and five females, or a predominance of females.

Camerano in the following year published several tables showing the parasites obtained from *Blaps mucronata* in the neighborhood of Turin. These tables show that he also found no predominance of males over females.

In the parasitic forms obtained during the present investigations I have been unable to find any difference in the number of specimens of the two sexes.

So far as the parasitic forms are concerned, then, there is in literature no evidence of any real difference in the number of males and females produced. It is merely necessary to explain the difference observed in case of free living specimens.

The results of Mühldorf have already been mentioned. In the collections of *Gordius robustus* made during these investigations I have usually obtained a slight predominance of females over males, only in a few small collections was a predominance of males present. In the collection of *Paragordius varius* made at Urbana the females were far more numerous than the males. At Douglas Lake, however, the reverse was true. Most of the collections made along the shore of the lake contained very few females.

The explanation must be sought in the behavior of the animals and not in any real difference in the numbers of the two sexes. The specimens in the older collections were obtained mostly accidentally and were either specimens that had just left their hosts, or were in the act of migration, or specimens that had not found a normal resting place. Since males are as a rule more active than females and more seldom come to rest in secluded places, as do females during the egg-laying period, it is but natural that they were the ones most commonly obtained in random collections. The results of Meyer are easily explained on this basis as he obtained his specimens by collecting in open water or dredging at the bottom of ponds. In those locations he would get nothing but migrating specimens, chiefly males. Mühldorf made most of his collections in small bodies of water where the females could not seclude themselves and he obtained no real difference in numbers. My own collections of *Gordius robustus* were made chiefly at the egg-laying habitats of the females and consequently there was a slight predominance of females. Since in this species the males have a habit of remaining for the greater part with the females the predominance was not very large. This also explains why very few specimens of *Gordius robustus* are obtained in general collections. The males of *Paragordius varius* are more active in nature and consequently very few of them were taken at Urbana, but they are more frequently obtained in general collections. At Douglas Lake I did not succeed in finding the habitats of the egg-laying females and as a result the females obtained were chiefly those that had just escaped from their hosts. A few were obtained that had settled down on grass near the shore to lay eggs.

Nothing very definite can be said about the seasonal variations of the Gordiacea as reported by previous workers. The present investigations indicate that the seasonal distribution depends more on the life cycle of the host than on the habits of the Gordiacea themselves.

The egg-laying habits of the females and the possible protection of the eggs by the adults require some further explanation. Villot (1874) des-

cribes to some extent the egg-laying habits of several species. Other workers have made smaller contributions to the knowledge of that subject, but have usually assumed that the observations obtained on the particular species at hand must hold true for all members of the group. Since in most cases also the identifications of the material at hand were obviously erroneous, such reports have done little more than add to the confusion that exists. One of the most recent of such reports is that of Wesenberg-Lund (1910). Some of its errors have already been pointed out by Mühlendorf. This writer, however, does not himself distinguish clearly between the habits of the different species under his observation. From my own observations it is clear that Wesenberg-Lund observed two different species, that he described the egg strings of one species, which he did not identify, and based his conclusions in regard to the protection of the eggs on what he observed in another species, which he identified as *Gordius aquaticus*.

Of the first species he obtained a single specimen with a long string of eggs wound around the stem of a plant. The male is absent and from the illustration given it is evident that the female has no protective instinct, as the eggs are uncovered and partly deserted by the female. From the character of the egg string and the habits of the specimen it is evident that the latter belonged to Chordodes, Parachordodes, or Paragordius.

In the case of the second species several masses were observed, but the egg strings were not described. Both males and females were present in the mass that was examined and pieces of egg strings were found when the mass was separated later in the season. Had Wesenberg-Lund separated a mass earlier in the season he would also have found nothing but pieces of egg strings. These specimens belonged to *Gordius aquaticus* or a closely related species which never lay long strings of eggs.

In regard to the supposed protective instinct of the parent Gordiacea my observations confirm those of Villot and Mühlendorf, who were unable to find any evident attempt on the part of the parents to protect their eggs. In nature the specimens of *Gordius robustus* usually remain with their eggs as in the case of the specimens observed by Wesenberg-Lund. In captivity this species seldom lays eggs and if it does it pays no attention to them, but allows them to drop to the bottom of the aquarium in small fragments. When disturbed in nature it does not hesitate to abandon the eggs. It remains with the eggs not because it tries to protect them, but merely because there is no stimulus to cause it to move on. In case of *Paragordius varius* the male does not remain with the female even when undisturbed in nature. The female usually remains with the eggs, but I have also found cases in which the eggs were deserted. Even when the female remains with the eggs it usually does not surround them, but merely remains in the same vicinity because it has become sluggish. This type of behavior is

indicated by the figure of the first specimen described by Wesenberg-Lund. In neither case can one speak of a true protection of eggs or young by the parents. Indeed, in case of the specimens observed by Wesenberg-Lund in the close masses it is very likely that most of the eggs had dropped to the bottom of the pond long before the larvae were ready to hatch.

#### *Behavior of larvae*

Little is known to the present time in regard to the habits of the larvae, except that they penetrate the tissues of a great many animals and in most of them become encysted and perish later. Cort (1915) even found such encysted larvae in trematodes. Villot (1891) and Camerano (1897) conclude from their own observations that such encysted forms are invariably lost and can not undergo further development. My observations on *Gordius robustus* show that an encysted stage in that species is not necessary and also that larvae that have lived free in the water for some time are usually incapable of development.

#### *Infection and intermediate host*

It is possible in the light of the present evidence to show that some of the former theories of infection are not tenable. The most commonly accepted theory in Europe has been that which assumes an active migration of the *Gordius* larvae into the larvae of aquatic insects or into other soft bodied aquatic animals and a consequent passive migration into a second host, usually an aquatic insect, which devours the first host. This theory finds its support again in the recent preliminary account of the life history of *Gordius tolosanus* published by Hans Blunck. He differs from the older views in that they assume that the adult Dytiscus, to mention a specific case, devoured the infected first host while he claims that the larval Dytiscus ingests the first host and becomes infected. The older theories seemed very logical in cases where the final host was an aquatic carnivore, but were difficult to apply where it was a supposed herbivore like a grasshopper or a cricket. Montgomery supposed in such cases that the first hosts were perhaps Mayfly larvae, that the encysted parasites were carried out of the water by the emergence of the Mayflies, and that they were liberated at the death of the insect, remained for a time on grass or leaves, and were taken into the final host with the vegetable food. Even as late as 1904 he had not discovered that *Gryllus abbreviatus* (*assimilis*), which he knew to be the host of *Paragordius varius* is not only an omnivore but a cannibal and that it is fond of its nightly bath. Assuming that the host is truly terrestrial, he went so far as to undertake experiments on desiccation of worms that had just emerged and to formulate theories in regard to the chances a worm deposited on dry land had for getting back to the water. Observations made during the present investigations show that all hosts of both species of Gordiacea here considered are neither truly terrestria

nor truly herbivorous. There is then, so far as the habits of the hosts are concerned, no reason why the infection should not take place as indicated in the earlier papers of Villot and Camerano and in the reports of most other writers. But the later conclusions of Villot and Camerano did not agree with the older views, neither do the results of the present investigation bear them out. Those views have obtained their greatest support in the report of Blunck. But since he does not submit the facts upon which his conclusions are based it is impossible to know at present whether the larvae that developed in the young stages of *Dytiscus* were encysted forms that the insect had devoured with prey or whether they were larvae that had merely adhered to the food or had even bored thru the external covering of the insects and thus actively migrated into them. The mere fact that he observed encysted larvae in the prey of the larval beetles would in no way constitute a proof of the fact that these encysted forms were identical with the parasitic stages found later in the beetles. The actual evidence presented up to the present time indicates that there is in the life history of the Gordiacea no encysted stage and no change of hosts. However, different species of the group may differ in this respect.

#### *Developmental period*

The conclusion of Švábentík, that the young forms must live several years in the bodies of the insects, is not confirmed by the present report. Blunck also does not indicate that the developmental period is very long, as he states that the parasites usually emerge soon after the beetle has attained its adult form.

The theory of Villot, Camerano and others that the Gordiacea frequently leave their hosts before the cuticula is completely formed has in no way been confirmed in the present work. On the contrary, the observations show that in the species investigated no essential change takes place in the cuticula after the specimens have emerged. The theory was not based upon observations made on the same specimens but merely upon the fact that certain specimens presented slightly different cuticular structures than did others. These differences may have been due to the fact that the specimens developed in different host species or in the same host species under different conditions. The placing of small or light colored specimens in the category of young individuals is based upon no scientifically established facts. The present observations show that the statement of Villo<sup>+</sup> that young specimens of *Gordius villoti* have a smooth cuticula and that the bristles develop later is founded upon error. Either the smooth individuals belong to a different species from the ones with bristles or the European species is variable in regard to that character.

#### ORGANOGENY

In regard to the organogeny the work of Vejdovsky (1894) stands almost alone. The contributions of Villot on that subject are of little

scientific value. His specimens were rendered unfit for histological investigation by the methods he employed in removing and killing the parasites. As proof it is merely necessary to consider his figures and interpretations of the hypoderm. I have obtained essentially the same results in specimens that were removed in water and were not properly killed. In that case the cells shrink and appear as small, deeply staining bodies with the intercellular bridges forming radiations from these centres. The whole mass appears as a network such as Villot (1874) has figured.

Even Vejdosky's work is not free from similar defects. The figures of the degenerating nuclei are certainly nothing more than those of poorly preserved nuclei in which parts of the nuclear structures had been macerated out. Naturally different stages of such a process would be found. He supplies part of the evidence for that himself in stating that the specimens obtained from Camerano, which were preserved in alcohol and were otherwise in very poor condition, gave him the best results in the study of these stages in the nuclear changes. Vejdosky was handicapped in many ways. He was unable to cut sections less than  $20\ \mu$  thick and had at his disposal no better stains than the carmins.

In regard to the morphology of the adults all the papers except those of Montgomery, Vejdosky, Rauther and Švábeník are of little scientific value because the investigations were either too fragmentary or they were carried out under conditions that could produce no accurate results. The present investigations show that all conclusions based purely upon adult structures are subject to verification. It is impossible to interpret properly the adult structures of the Gordiacea without knowing something about their development.

### *Metamorphosis*

Altho the present work gives some information in regard to the metamorphosis of the two species studied, there are many questions that still remain unanswered. There exists no previous literature on this subject. Montgomery (1904) and after him Mühldorf assumed that the proboscis of the larva is a precephalon and does not take part in the development. The present investigations show that this is not the case, but that the brain of the adult in both of the species examined develops from the posterior part of the proboscis, and that even the cord of tissue connecting the stylets with the partition between proboscis and body, representing possibly the larval esophagus, develops in one of the species.

The present investigations have also for the first time revealed the fact that the larval cuticula is shed when the parasite attains its full development and that the remnants of the larval proboscis which do not take part in development are lost with the larval cuticula.



### *Later development*

The later development in both species consists of uninterrupted growth and differentiation from the time the first rudiments of the organs of the adult appear to the time the parasites are ready to leave their hosts.

The question of what constitutes a larval stage in the Gordiacea has become even more complicated thru the present studies. Villot regarded the larva as an embryo and designated the parasitic stage as larva. Nearly all other writers have considered the stage that is free living after leaving the egg as larva and the later stages as developmental, young or juvenile. The application of the name larva to the parasitic stage was regarded as incorrect because it had no remnant of the earlier larva except the degenerated proboscis and there was no definite change that marked the transition between this stage and the adult. The discovery of the larval cuticula and the fact that it is shed at the time the parasite becomes ready to leave its host removes to a great extent the objections to the application of the term to the parasitic stage, and the term larva used to designate all the stages from the time the free living form emerges from the egg to the time the parasite is ready to leave the host would certainly be justified. But since the free living and the parasitic stages are in many ways completely different, I have used the term larva in this paper to designate only the free living form and have used for the other the term parasite or parasitic stage. The term embryo is incorrectly used when applied to the free living form. The other terms for the parasitic stage have for the most part been avoided in this paper because they are misleading. The term juvenile can be applied to any other stage except the adult. The term developmental can just as correctly be applied to the embryological stage as to the parasitic.

*Cuticula.* During the entire developmental period the larval cuticula expands and also increases in thickness. In that respect it differs from the cuticula of arthropods.

The fibrous cuticula of the adult is in neither of the species a secretion of the hypoderm, but a differentiation of the upper parts of the cells, as was already pointed out by Rauther. In other respects the cuticula in the two species is formed very differently. In *Gordius robustus* there is an intermediate layer formed between larval and the adult cuticula, the non-fibrous cuticula is laid down before the fibrous cuticula begins to be formed, the bristles are projections of the fibrous cuticula, and there are no evident protoplasmic connections between the non-fibrous cuticula and the hypoderm. In *Paragordius varius* the larval cuticula remains in contact with the non-fibrous cuticula, the structures of the non-fibrous cuticula are laid down by protoplasmic strands that extend up to it from the hypoderm and are present even in the adult, and the bristles or tubercles are structures of the non-fibrous cuticula. The larger radiating fibers that form the

bristles in *Gordius robustus* may be homologous with the protoplasmic strands in *Paragordius varius*, but they do not appear to retain living substance in the adult condition.

Montgomery states that he failed to find any strands of protoplasm passing thru the fibrous cuticula of *Paragordius varius* but found granules in the fibrous cuticula of the male in the region where the tubercles are present. He also figures branching roots for the tubercles. His method of staining for a long time with iron hematoxylin would not readily bring out continuous fibers. What he figures as granules in the fibrous cuticula are undoubtedly nothing more than the ends of some of the protoplasmic strands which in that locality are very large. The roots of the tubercles can be nothing else than several pieces of strands which he could not trace accurately and consequently regarded as passing to the same tubercle. The protoplasmic strands in the cuticula have been figured for other species of Gordiacea, and Vejdovsky (1894) shows them in definite relation to the areolae.

*Hypoderm and nervous system.* It is impossible within the space of this paper to discuss the minor differences that exist in the descriptions of the hypoderm. Some of the artifacts in the figures of Vejdovsky have already been pointed out.

The development of the nervous system requires no further discussion. In the structure of the nerve cord a minor difference appears in the two species studied, in *Gordius robustus* the neural lamella consists of a series of cells while in *Paragordius varius* all the cells are located in the cord itself and only fibers connect the cord with the hypoderm. The subneural canal of Vejdovsky was probably an artifact due to the separation of the hypoderm cells at the point where the fibers from the cord enter. Rauter regarded most of the large cells of the nervous system as belonging to the supporting tissue. That is certainly an error.

The mass of cells in *Paragordius varius* designated by Montgomery as retina must be regarded as the major part of the cephalic ganglion.

*Alimentary canal.* The favorite textbook doctrine that the alimentary canal of the Gordiacea is well developed and functional in the parasitic stages must be regarded as disproved. Vejdovsky has already pointed out that there is no difference in the essential structure of the alimentary canal in the young forms and in the adults. He, however, was unable to trace the origin of the anterior part of the tract, as the youngest specimens examined by him were at the stage where the adult cuticula begins its formation and were in such miserable state of preservation that he was unable to locate the gonads in them. Evidently the entire interior had become disintegrated. He found the larval proboscis at the point where the mouth should have been, but in spite of that regarded the mouth as open. In his forms the larval esophagus underwent even more development

than in *Paragordius varius*. The brown gland which he found in the region of the esophagus is either homologous with the part of the larval esophagus of *Paragordius varius* that grows over the intestine or else is homologous with the anterior glandular part of the intestine itself. The latter has been the opinion of Montgomery and others who have studied the larva. From the present investigations it is evident that the mouth does not become open until the adult stage is reached. In *Gordius* it never becomes open; for the connection between the larval esophagus and the intestine is severed at the very beginning of the parasitic stage and no opening can be present after that. It was upon examination of sections of *Gordius robustus* that Ward (1892) made the positive assertion that in the specimen examined there was no trace of an esophagus. Others have obtained similar results in this and related species. Thus Rauther in the form he designated as *Gordius aquaticus* states that he still finds the mouth opening as a thin chitinous tube, but fails to find any trace of an esophagus. Švábenský states that in *Gordius montenegrinus* the alimentary canal is very degenerate. Both of these species are very closely related to *Gordius robustus*.

There is a regression in the cells of the alimentary canal when the adult stage is reached, but it is not much more pronounced than the regression that begins at the same time in the other tissues.

The cilia mentioned in the cloaca and genital tubes in the reports of Montgomery and Rauther have been explained in the description of *Paragordius varius*. Rauther also figures cilia for the intestine of *Gordius tolosanus*. His description, however, explains his error. He states: "In der kaudalen Darmregion von *G. tolosanus* war auch deutlich zu beobachten, dass die freie innere Oberfläche des Epithels einen sehr regelmässigen fibrillär struierten Saum trägt, der offenbar aus kurzen Cilien besteht." What he observed was nothing more than the inner differentiated zone that was in some cases found in *Gordius robustus* in the present investigation. It is this type of theoretical interpretation found everywhere in Rauther's paper that makes his conclusions almost worthless. Fortunately he has usually given his actual observations before interpreting them. I have found no cilia in the intestine of either of the species studied in any stage of development.

Another case of Rauther's interpretation is his defense of Vejdosky's statement that the male cloaca is evertable and serves as a bursa copulatrix. He defended Vejdosky's statement in an attempt to explain the bristles around the anus of the male, in spite of the fact that he knew that it had been contradicted by Camerano, von Linstow and Villot, and that he had observed no evidence to prove its correctness. But, the figure given by Vejdosky (1886, Fig. 31) shows conclusively that the structure at the anal opening can not possibly be the everted cloaca. He shows the cloaca still in place and the cellular part ending at the anus. The part extruded was evidently a mass of spermatozoa.

*Muscles and parenchyma.* The very close relationship between muscle and parenchyma cells is evident from the descriptions of both of the forms studied. In the very earliest stages observed there is no distinction between muscle cells and mesenchyma cells that later make up the parenchyma. The longitudinal muscle cells can of course from their position be distinguished in a general way from mesenchyme cells; but in many cases cells appear that are partly within and partly without the muscle layer, and on account of the existence of all degrees of intercalation, must be interpreted as belonging to the mesenchyma. Furthermore, the cells that line the hypoderm which later forms the nerve cord are at the earliest stages not distinguishable from the muscle cells lining the rest of the hypoderm. In case of the cloacal muscles all gradations can be found between unmistakable muscle cells and regular parenchyma cells. All of these muscles except the radiating muscles surrounding the posterior part of the cloaca of the male develop from mesenchyme. The radiating muscles develop from the muscle cells lining the hypoderm that is inturned at the cloaca. From these facts it seems probable that both muscle and parenchyma cells develop from mesenchyme and that the position rather than any inherent properties of the cells determines whether they are to form muscle or parenchyma cells.

The fibrils in the longitudinal muscles do not appear until the adult stage has nearly been reached. Normally they arrange themselves in a row completely surrounding the rest of the cell, but in cases of excessive flattening they may appear to be interrupted at the outer edge. Such cells formed the basis of Vejdovsky's contention that the muscles of the Gordiacea are open toward the hypoderm.

In the light of the present investigations the descriptions of the peritoneal linings of epithelial nature must be regarded as resting upon misinterpretations. Vejdovsky was the most positive advocate of the theory that the parenchyma layers are to be interpreted as true epithelium. Villot (1881, 1887) discovered the true origin of the parenchyma layers, but his interpretation was not universally accepted because it lacked conclusive proof. Von Linstow (1889) also believed that no true epithelium was present. Most other workers were not inclined to give any positive statements, except Švábenský, who followed the footsteps of Vejdovsky, and, altho his figures show nothing that contributes in any way to the knowledge of the subject, asserted in the most positive terms the existence not only of true epithelium, primary and secondary body cavities, but also a rudimentary segmentation of the body cavity.

The present investigations show that in the early stages there are no epithelial layers except the hypoderm and the intestine, that the muscles and parenchyma arise as mesenchyme, and that the mesenteries and peritoneal linings are nothing more than layers of parenchyma. The

cavities present are not true coelomic cavities, but remnants of the blastocoel or primary body cavity. The intestine adheres to one side of the cavity, but is not covered by the peritoneal lining. In the early stages the gonads also are not covered by parenchyma.

The two species investigated differ widely in the distribution of the mesenchyme in the female. In *Gordius robustus* the mesenchyme does not surround the ovaries while in *Paragordius varius* it completely surrounds them.

Vejdovsky was unfortunate in his investigations in that the earliest stages at his disposal were those in which the mesenchyme had just completed the formation of the lining of the muscles and the covering for the gonads. At that stage it appears more like true epithelium than at any other. In his specimens the appearance was even more that of true epithelium because the looser mesenchyme cells were not preserved.

No true circulatory system is present, but the body cavities may be regarded as chambers that aid in the distribution of liquids in the body.

No trace of a special organ for excretion is present. Montgomery found in one female an elongated organ passing along the dorsal side of the anterior part of the intestine and at intervals giving off branches. He regarded this as the vestige of an excretory organ and described and figured it in detail. Indeed he described it so well that his error in interpretation is easily detected. The structure was nothing more than the mycelium of a fungus, such as are often found in older specimens. Montgomery himself states that "it is most remarkable that this organ appears to possess no nuclei of its own. Small deep-staining nuclei are found in it (about 29 in number), but from the close resemblance of these to the nuclei of the parasitic organisms found in the lumen of the medio-ventral canal, they certainly belong to such parasites which have penetrated the walls of the organ."

*Reproductive organs.* The origin of the germ cells must still remain a mystery. That the bodies found by Schepotieff in the larval stage at the sides of the intestine are really the primordial germ cells is very doubtful both from the appearance of similar bodies in other species and from his own description. In the larvae of *Paragordius varius* examined by me similar bodies were present. Montgomery figures two bodies, a smaller one anterior and a larger one posterior, but states that more may be present. In the specimens examined by me there were present invariably the larger posterior body, which undoubtedly is a part of the intestine filled with a substance of nearly homogeneous nature, and two smaller, spherical bodies with deeply staining centers, attached to the antero-lateral edges of the larger body. Montgomery regards the substance included in the bodies as excretory in nature. In *Gordius robustus*, where two bodies appear that answer more closely to the descriptions and figures of Montgomery, these

bodies disappear in the later stages and the intestinal wall in that region becomes built up of large cells. In *Paragordius varius* I have found no trace of the disappearance of the bodies in larvae that had lived in the free condition for a long time.

Schepotieff in his description says that the bodies are formed from a vesicle which arises from the dorsal side of the intestine. He states that they are vesicles composed of walls filled with a gelatinous, feebly staining, homogeneous mass. Each wall he believes to contain two flattened nuclei. He thought this structure was similar to that of the reproductive tubes of the adults. The present investigation, however, has revealed that the gonads in the early stages are composed of cells of an undifferentiated nature and consequently it is doubtful that they are derived from larval structure of such specialized character.

The reproductive organs in the two sexes arise in the same manner and are differentiated only later in development. The term germinal epithelium is hardly applicable to the early rudiments of the gonads. Even in later stages, with the exception of the efferent ducts, no part of the reproductive columns contains a structure that in any way resembles epithelium. The resemblance of the walls of the oviducts and sperm ducts to epithelium has been described by others. Rauter assumed from analogy with similar structures in other animals that the gonads in this group must arise as evaginations of some epithelial structure, and believed that the epithelial remnants presented by the oviducts indicated that the evagination had taken place at the point where the oviducts enter the cloaca. The results of the present investigation show that this theory does not hold. The gonads appear some time before there is any trace of an evagination in the region that later forms the cloaca. The connection between gonads and intestine is only secondarily acquired. Moreover, the epithelial structure of the oviducts is not a remnant of a previous epithelial covering of the gonads, but a secondary structure formed by the rearrangement of cells that in the early stages show no indication of an epithelial nature. It is possible, of course, that the gonads do arise from the posterior end of the intestine, but in that case they are at first completely cut off, their origin being more like that of mesenchyme than of mesothelium, and are later reunited.

In later stages the ovaries are still essentially like the testes, except that the lower walls have become distended at intervals to allow for the growth of the ova. The entire ovarian contents are transformed into germ cells and consequently the membranes containing them have usually been regarded as egg reservoirs or uteri. Even Montgomery, who was aware of the true nature of the dorsal tubes, retained the name uterus for them. He believed that the eggs at the time of laying pass back into those tubes and backward along them to the oviducts. That, however, is an error. In

*Paragordius varius* some of the eggs are retained in these tubes and later pass back along them to the oviducts, but the majority of eggs are contained in the ovarian buds and are liberated by the rupture of the membranes, pass back along the tubes formed by the parenchymatous walls which form the mesenteries, and enter the oviducts when they reach the posterior end. In *Gordius robustus* no eggs are retained in the primary ovarian tubes and all pass back along the body cavity. It is evident from the descriptions given in this report that the only name applicable to either a primary ovarian tube or the ovarian buds or both together is ovary.

The budding of the ovaries, which by Vejdovsky and Švábeník was regarded as rudimentary body metamerism, was found in the species examined to be highly irregular and not opposite in the two ovaries. Consequently it can be regarded as no more of an indication of true metamerism than the branching of the intestine in the polyclads or of the uterus in some of the larger cestodes.

#### PHYSIOLOGY

The functions of the organs in the Gordiacea are practically unknown. Interpretations have usually been made from analogy with similar organs in other groups, rather than from actual observations. But in an isolated group like that of the Gordiacea such interpretations are very unreliable. In the present investigations certain observations have some bearing on the possible functions of some of the organs and the interpretations are given here more as possibilities than as certainties.

*Nutrition.* The absorption of nutritive substances seems to be carried on by the entire outer body surface. In the younger stages of *Gordius robustus* the hypoderm cells appear also to secrete a digestive substance that attacks the cells of the surrounding tissues of the host. Thus the young specimens enclosed in the tissues of the hosts in the later stages are always found in larger pockets formed by the digestion of the cells immediately surrounding the parasite. The digestion does not appear to take place at any one point of the body of the parasite, but occurs simultaneously at all points. In later stages even in *Paragordius varius* it seems impossible that any capillary tube that may form the anterior opening of the intestine could supply a large enough quantity of fluid from the body cavity of the host to feed the developing parasite. In *Gordius robustus* that is entirely out of the question, as in that species there is clearly no anterior opening to the intestine.

*Excretion.* The conclusion that the hypoderm and not the intestine carries out digestive functions in the parasite leaves the high stage of development of the intestine entirely unexplained. It is, however, not necessary to look far for the probable function of the intestine. It fulfils every requirement of an excretory tube. The resemblance of its structure to that of the Malpighian tubules in insects is very close, as I had sufficient

opportunity to observe in the search for young parasitic forms in sections of hosts. The tube is either nearly or entirely closed at the anterior end and widely open at the posterior end.

Since the fluid in the body cavity of the insect is itself partly excretory in nature it is difficult to understand how a large parasite can live in that fluid and possess no trace of an excretory system.

Meissner already regarded the intestine as an excretory tube, but did not recognize its true ontogenetic position as a part of the alimentary canal. Montgomery regarded the bodies enclosed in the intestine of the larva as excretory in nature.

*Functions of the nervous system.* All reactions in the two species observed are of a very low nature. The most definite response observed is the grasping reaction of the male when in contact with the body of the female. All other responses consist merely of motion, the degree of motion depending both upon the magnitude of the stimulus and the state of activity of the specimen. In case of specimens at rest it usually requires several successive stimuli to produce any great irritation. There is no direct response to light in case of free specimens, but the difference in the activity of the specimens at different times of the day may be partly due to the difference in the light intensity. The most definite case of orientation to light is the orientation of the developed specimens in the abdomen of the host so that the anterior end is always at the point of exit. This orientation may, however, be in part due to some other agent. The emerging reaction on contact with water is next to the grasping reaction of the male the most definite response to stimuli, but the reaction here is also nothing more than motion.



## RELATIONSHIPS

The results obtained in the present investigations afford new evidence both in regard to the interrelationships of the group and their relations to other groups.

From the descriptions given in this report it is evident that the two species studied differ widely in regard to the form and structure of the larva, the participation of the proboscis in later development, the arrangement of the parenchyma in the female, and the development of the adult cuticula. An examination of the literature shows that these differences are not confined to the species studied, but appear in the same grouping in all cases where sufficient information is at hand to permit comparison. I have myself examined larvae and also sections of adults of *Chordodes* sp. and find an essential agreement in structure with *Paragordius varius*. The larva of *Chordodes* is even more abbreviated than that of *Paragordius*, the cuticular structures and the mesenteries are more pronounced, and the esophagus is present in the adult.

In view of these differences I believe that there exist in the present family of Gordiidae two well defined, natural groups, one of which is represented by the genus *Gordius* and the other by the three genera *Chordodes*, *Paragordius* and *Parachordodes*. For that reason I propose to retain the family Gordiidae for the genus *Gordius* and to establish a new family, *Chordodidae*, for the other three genera.

Since the position of the present family of *Nectonemidae* is not definitely established, and since from the descriptions given *Nectonema* resembles the nematodes and especially the *Mermithidae* in the structure of the muscle cells, the alimentary canal, the hypoderm with its longitudinal thickenings and lack of cell boundaries, the structure of the cephalic ganglion, and in the location of the nerve cords within the thickening of the hypoderm, it is not possible to retain the *Nectonemidae* in the order Gordiacea. The family may for the present be assigned to an independent position in the vicinity of the *Nematoda*.

The limits of the old family Gordiidae then become the limits of the order Gordiacea.

The description of the proposed family Gordiidae may be given as follows: Gordiacea with a smooth cuticula, presenting no true areoles. Bristles on the body arising from the fibrous cuticula. Mouth, when cavity is present, not connected with the intestine. Ovaries not enclosed by mesenchyme and consequently no double mesenteries in the female.

Posterior end of male provided with two projecting lobes or prongs arising a short distance behind the anus. A post-anal crescent is present and has its tips directed toward the prongs. Posterior end of female entire. Larva with elongated body and pointed posterior end. Only genus in family: *Gordius*.

The limits of the new family Chordodidae are the following: Gordiacea with rough cuticula, presenting true areoles. Tubercles and bristles arising from the non-fibrous cuticula. Ovaries enclosed by mesenchyme, consequently double mesenteries present in the female. Posterior end of male forked or provided with a dorso-ventral groove. Post-anal crescent absent. Posterior end of female entire or provided with three lobes. Larva with short body, rounded at posterior end and provided with postero-lateral spines. Genera included in family: *Chordodes*, *Paragordius*, *Parachordodes*.

The evidence presented in this paper shows clearly that the supposed relationship to the Annelida does not exist. True coelom and segmentation are absent. Other workers have already shown that there is in the development of the Gordiacea no trace of the trochophore larva of the Annelida. Almost the only thing in common for the two is the ventral position of the nerve cord and its passage around the esophagus.

The evidence for a possible relationship to the Nematoda is strengthened by the discovery of a moult in the development of the Gordiacea and by the establishment of the absence of cilia or a true coelom in that group. The absence of a complicated metamorphosis and the fact that the proboscis is not exclusively a larval organ remove some of the objections to such a relationship.

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### EXPLANATION OF PLATES

Plate I consists of photomicrographs made from slides. The other figures were drawn either from slides by means of a camera lucida or from photographs by means of a copying lens. Magnifications were obtained in case of drawings by the projection of the stage micrometer scale on the paper and in case of photographs by projecting the stage micrometer scale on the focussing screen.

The original thesis deposited in the library of the University of Illinois contains 656 figures, of which all but twelve are photomicrographs. Those photographs illustrate many points in the description that could not be shown in the drawings.

The author is indebted to the University of Illinois for special services from an artist of the university to draw a number of the figures. He is likewise indebted to the Zoological Division of the Bureau of Animal Industry at Washington, D. C. for permitting the artist of the division to draw a large number of the figures.

The abbreviations I 4, I 7, and I 8, as used in the descriptions of figures, are the serial numbers of the infection experiments and are described in the section on parasitism in *Gordius robustus*.

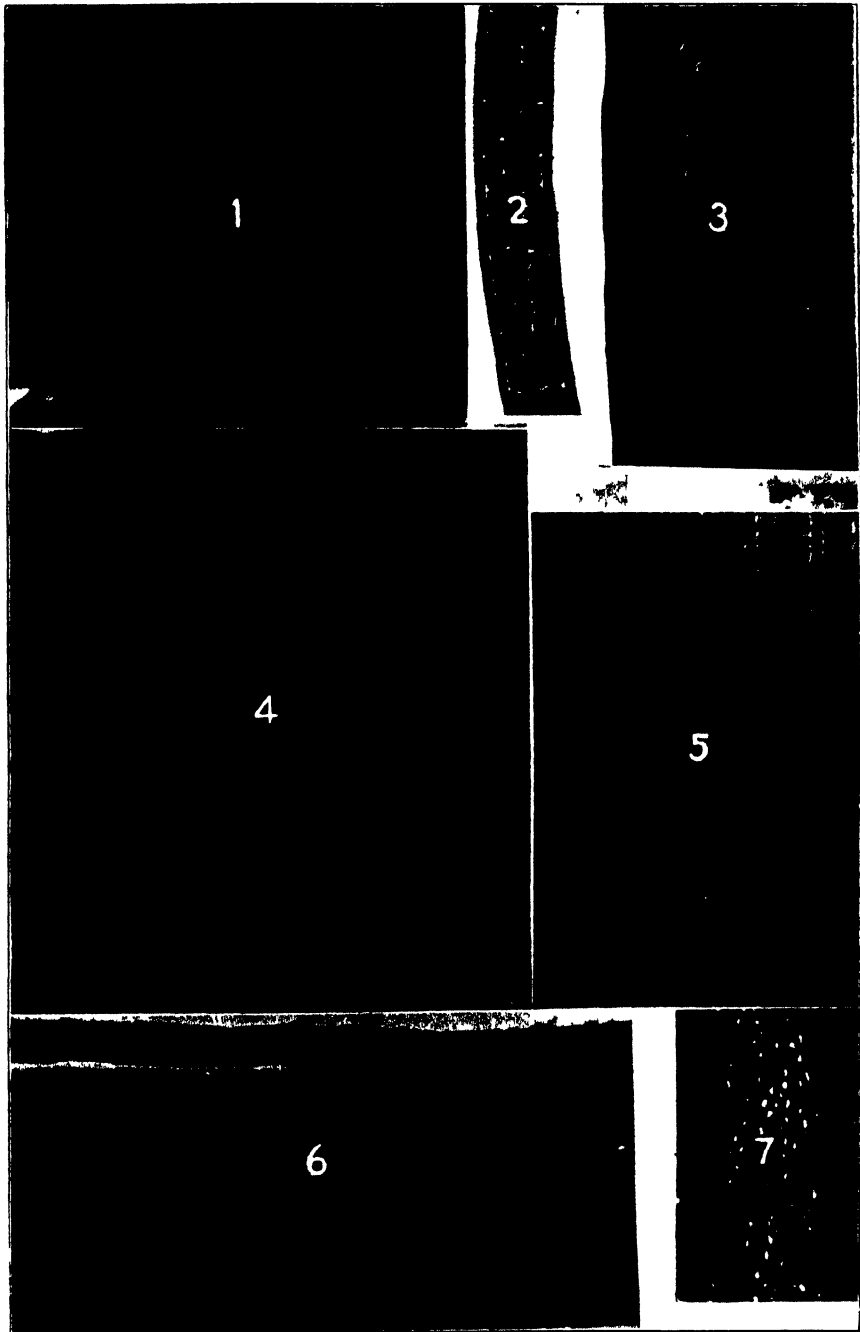
## PLATE I



## EXPLANATION OF PLATE

## PHOTOMICROGRAPHS OF MOUNTS

- Fig. 1.—*Paragordius varius*, tangential section of fibrous cuticula of adult; shows fibres, ends of radiating strands, and cross formed by the passage thru the cuticula of a large strand to a tubercle;  $\times 800$ .
- Fig. 2.—*P. varius*, longitudinal section of young female; shows that buds of ovaries are not opposite;  $\times 50$ .
- Fig. 3.—*P. varius*, longitudinal section thru anterior end of adult, showing large parenchyma cells;  $\times 100$ .
- Fig. 4.—*Gordius robustus*, thin layer of fibrous cuticula of adult after maceration with nitric acid;  $\times 1240$ .
- Fig. 5.—Same as Fig. 4;  $\times 175$ .
- Fig. 6.—*P. varius*, longitudinal section perpendicular to surface of muscle cells of adult; shows elongated condition of cells and nuclei;  $\times 150$ .
- Fig. 7.—*P. varius*, tangential section thru wall of cloaca, showing pores;  $\times 475$ .



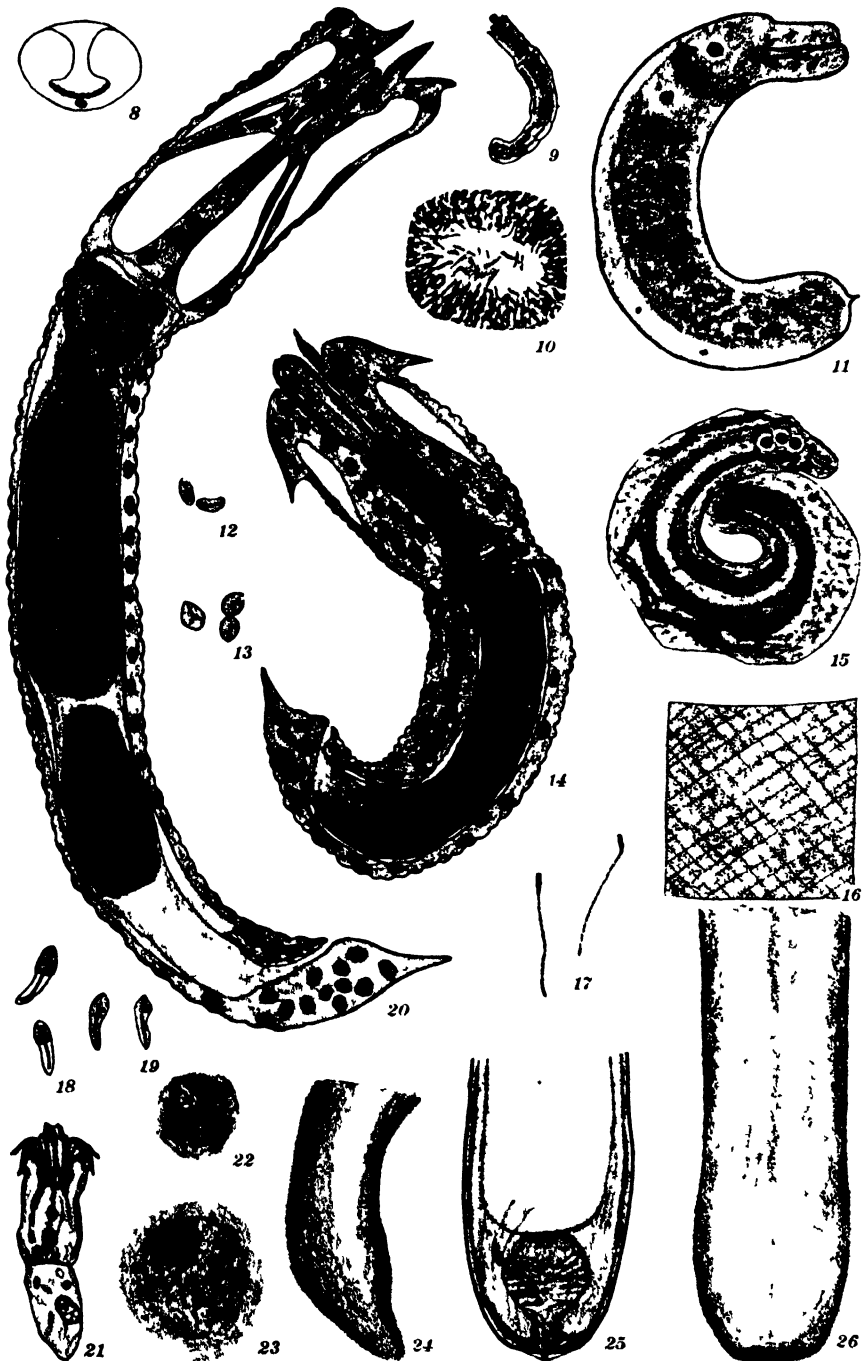


**PLATE II**

## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 8.—Posterior end of male; end view, slightly ventral; free hand sketch from alcoholic specimen;  $\times 20$ .
- Fig. 9.—Six day specimen from I 4; posterior end turned up and not shown;  $\times 250$ .
- Fig. 10.—Section thru sperm mass just posterior to anal opening of female; shows free area where spermatozoa have migrated into cloaca;  $\times 250$ .
- Fig. 11.—Six day specimen from I 4; large nuclei in anterior end of intestine;  $\times 385$ .
- Fig. 12.—Spermatozoa in anterior end of male in which the adult cuticula is not fully developed;  $\times 800$ .
- Fig. 13.—Spermatozoa from posterior end of same specimen as in Fig. 12;  $\times 800$ .
- Fig. 14.—Larva after prolonged free existence; side view; drawn in optical section from stained specimen cleared in oil of wintergreen;  $\times 1200$ .
- Fig. 15.—Eight day specimen from I 8; intestine with large nuclei at anterior end; cells in cephalic ganglion somewhat enlarged;  $\times 190$ .
- Fig. 16.—Adult cuticula; surface view, showing intersecting lines and light spots; drawn to scale from living specimen obtained from Mt. Vernon, Illinois;  $\times 30$ .
- Fig. 17.—Spermatozoa from seminal receptacle of female;  $\times 800$ .
- Fig. 18.—Mature spermatozoa from male;  $\times 800$ .
- Fig. 19.—Spermatozoa in section of adult male;  $\times 800$ .
- Fig. 20.—Larva just hatched; side view; drawn in optical section from stained specimen cleared in oil of wintergreen;  $\times 1325$ .
- Fig. 21.—Proboscis of free living larva; section;  $\times 800$ .
- Fig. 22.—Anterior tip of parasitic form, showing larval hooks;  $\times 240$ .
- Fig. 23.—Section just posterior to preceding;  $\times 240$ .
- Fig. 24.—Posterior end of white male, nearly adult; side view;  $\times 25$ .
- Fig. 25.—Posterior end of white female, nearly adult; semitransparent; side view;  $\times 25$ .
- Fig. 26.—Posterior end of adult female; dorsal view; drawn from alcoholic specimen;  $\times 25$ .





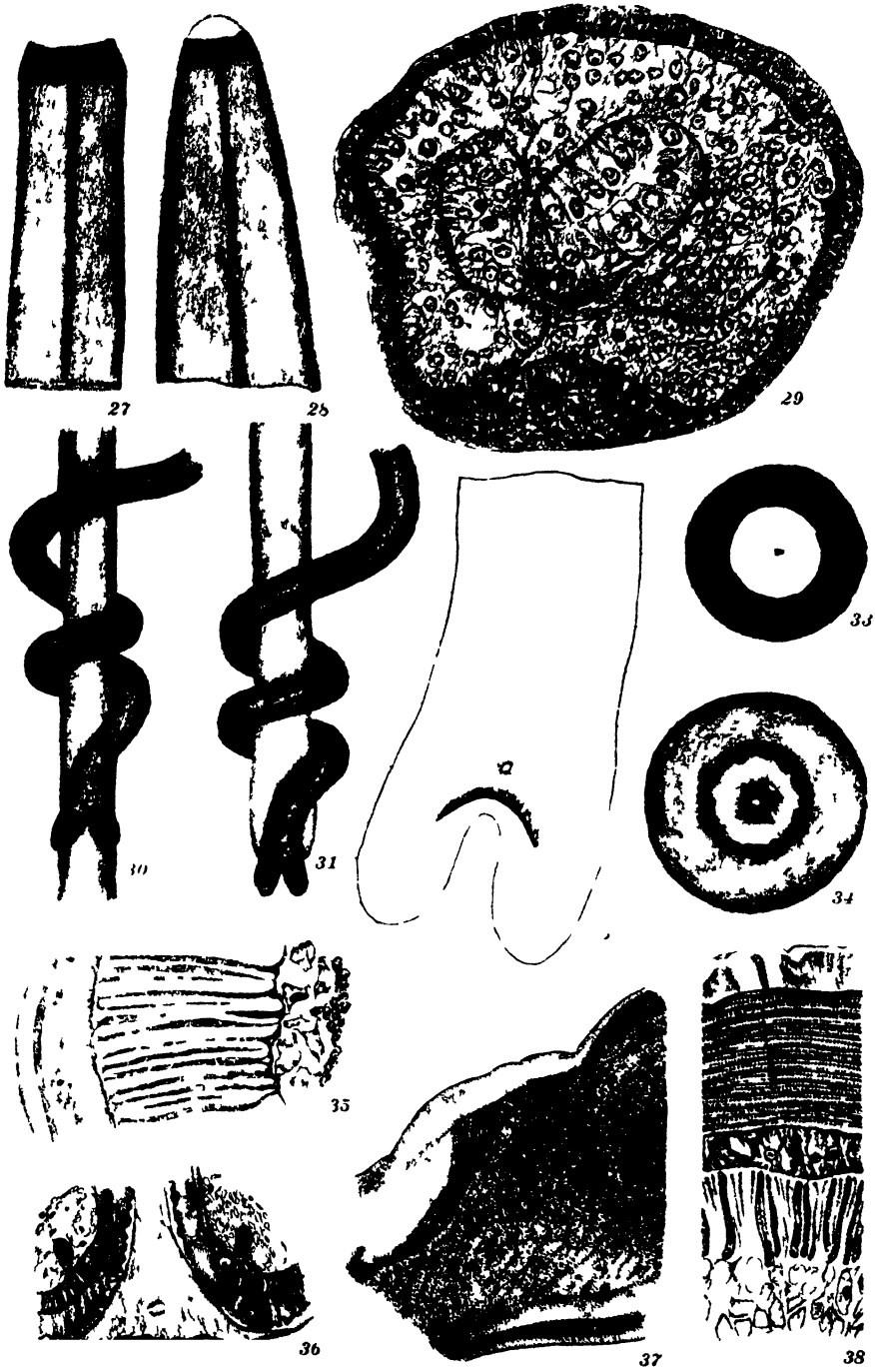
## PLATE III



## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 27.—Anterior end of adult male; dorsal view, drawn from alcoholic specimen;  $\times 25$ .
- Fig. 28.—Anterior end of female, Leidy collection of 1879; dorsal view; drawn from alcoholic specimen;  $\times 25$ .
- Fig. 29.—Section thru posterior end of young male, showing junction of sperm ducts and intestine;  $\times 360$ .
- Fig. 30.—Male and female; early stage in process of mating; sketch from living specimens;  $\times 10$ .
- Fig. 31.—Male and female; just before discharge of sperm;  $\times 10$ .
- Fig. 32.—Posterior end of adult male; ventral view; drawn from alcoholic specimen;  $\times 40$ .
- Fig. 33.—End view of anterior end; drawn from alcoholic specimen;  $\times 50$ .
- Fig. 34.—Posterior end of adult female; end view; drawn from alcoholic specimen;  $\times 50$ .
- Fig. 35.—Early stage in the development of adult cuticula;  $\times 480$ .
- Fig. 36.—Cross section thru base of fork of male; adult cuticula not completely formed; shows canal passing from end of intestine to outlet in larval cuticula at tip of fork;  $\times 120$ .
- Fig. 37.—Sagittal section thru postcloacal ridge of young male;  $\times 140$ .
- Fig. 38.—Structure of adult cuticula;  $\times 440$ .



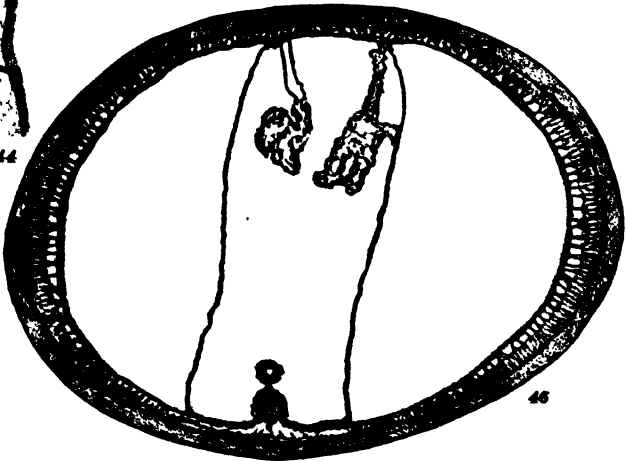
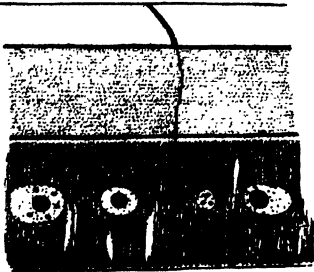
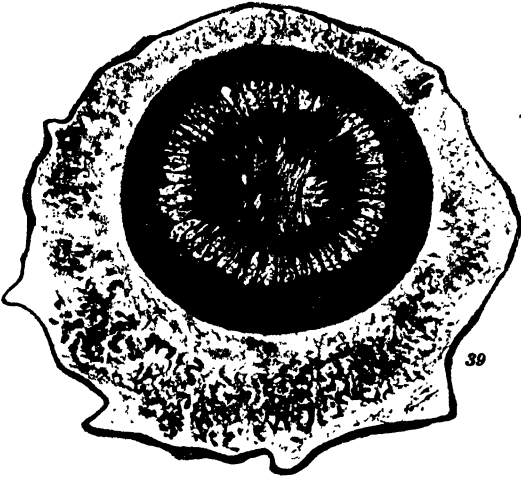


## PLATE IV

## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 39.—Cross section in front of cephalic ganglion in specimen shedding the larval cuticula;  $\times 90$ .
- Fig. 40.—Longitudinal section of specimen with adult cuticula nearly completed; shows spine in early development with minute fibre barely traceable to hypoderm;  $\times 870$ .
- Fig. 41.—Hypoderm and the formation of granular layer under larval cuticula;  $\times 500$ .
- Fig. 42.—Cross section of specimen with developing cuticula; shows nerve cell and fibre in hypoderm;  $\times 450$ .
- Fig. 43.—Stage in the development of adult cuticula later than that shown in Fig. 35; cuticula has attained about half its final diameter;  $\times 450$ .
- Fig. 44.—Late stage in development of adult cuticula, longitudinal section; shows bristle passing thru granular layer;  $\times 665$ .
- Fig. 45.—Section parallel to neural lamella in specimen nearly mature; shows bipolar cells;  $\times 320$ .
- Fig. 46.—Cross section thru body of female that has deposited its eggs; shows tissues partly degenerated;  $\times 135$ .





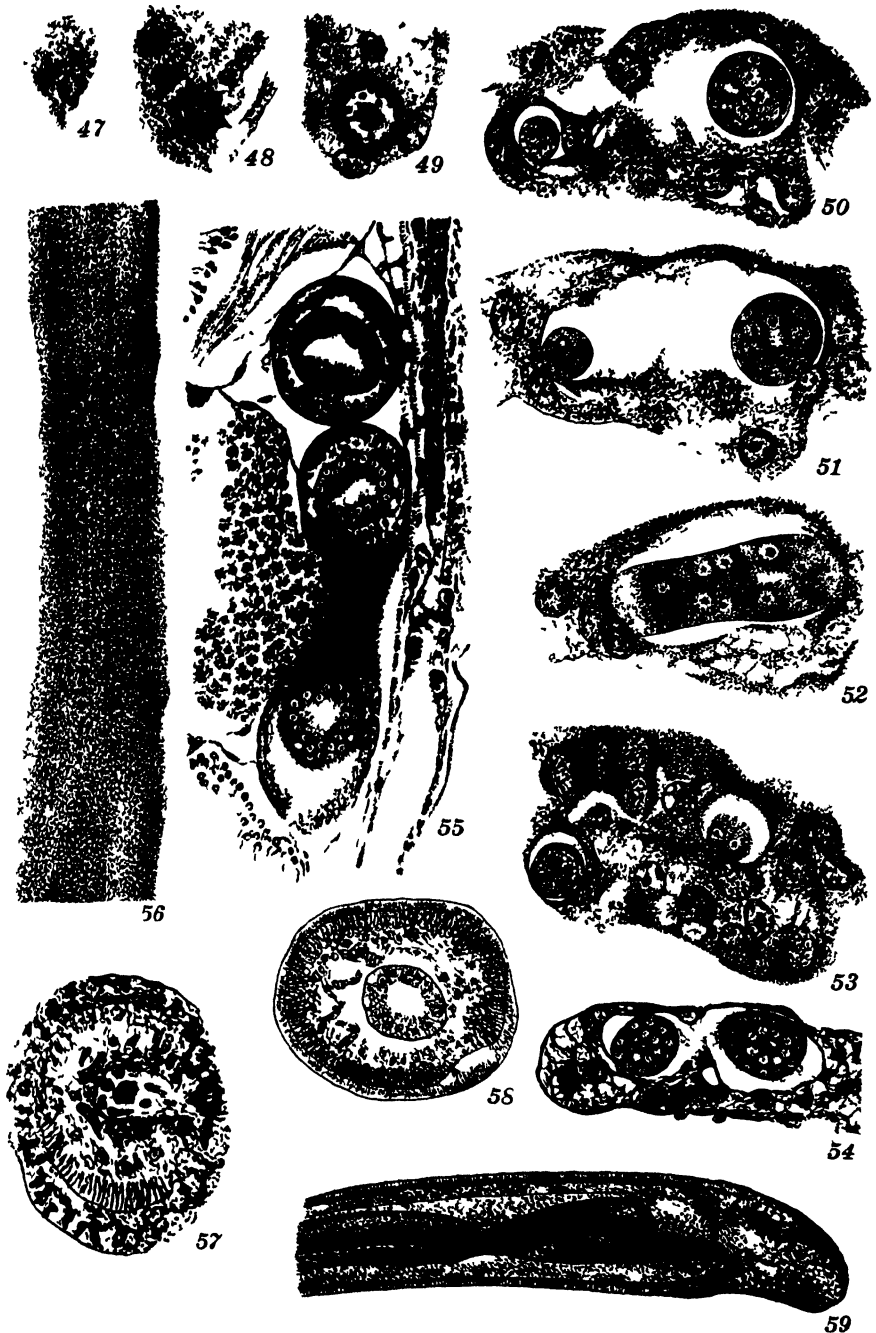
## PLATE V



## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 47.—Three day specimen from I 7; cross section of stylets in tissues of host;  $\times 640$ .  
Fig. 48.—Adjacent section posterior to Fig. 47; cross section of hooks of proboscis in tissues of host;  $\times 640$ .  
Fig. 49.—Adjacent section posterior to Fig. 48; muscles in proboscis;  $\times 640$ .  
Fig. 50.—Five day specimen of I 7; section thru anterior end and middle of body in tissues of host;  $\times 480$ .  
Fig. 51.—Section adjacent to Fig. 50;  $\times 480$ .  
Fig. 52.—Section adjacent to Fig. 51;  $\times 480$ .  
Fig. 53.—Section thru extreme ends of same specimen; hooks in proboscis;  $\times 480$ .  
Fig. 54.—Section of seven day specimen of I 7 in tissues of host;  $\times 225$ .  
Fig. 55.—Section of nine day specimen of I 7 in tissues of host;  $\times 225$ .  
Fig. 56.—Twenty-eight day specimen of I 8; tangential section thru hypoderm, showing the two rows of nerve cells;  $\times 220$ .  
Fig. 57.—Twelve day specimen of I 7; cross section thru anterior end, showing proboscis muscles;  $\times 400$ .  
Fig. 58.—Twenty-eight day specimen of I 8; cross section near anterior end;  $\times 220$ .  
Fig. 59.—Sagittal section thru posterior end of young male; anus still opens terminally;  $\times 70$ .



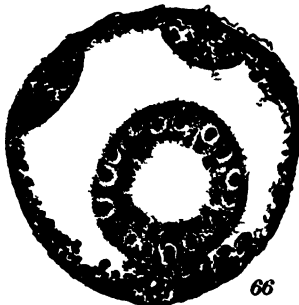
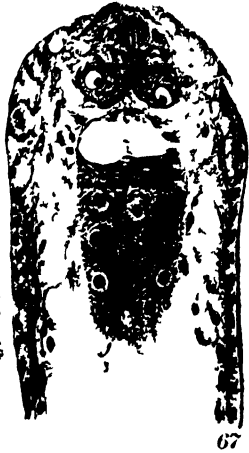
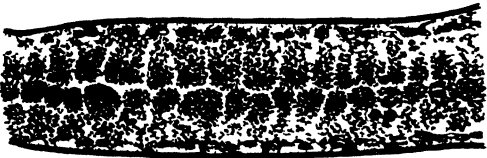


## PLATE VI

## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 60.—Sagittal section thru posterior end of young male; slightly older than that of Fig. 59,  $\times 70$ .
- Fig. 61.—Similar section thru still older specimen;  $\times 70$ .
- Fig. 62.—Young female; longitudinal section, showing budding of ovaries; buds not opposite;  $\times 55$ .
- Fig. 63.—Twelve day specimen of I 7; oblique section of posterior end, showing early intestinal diverticula where reproductive organs later join;  $\times 400$ .
- Fig. 64.—Similar section thru another specimen of the same lot;  $\times 400$ .
- Fig. 65.—Twenty-eight day specimen of I 8; cross section of posterior end, showing intestinal diverticula;  $\times 400$ .
- Fig. 66.—Twelve day specimen of I 7; cross section;  $\times 400$ .
- Fig. 67.—Twelve day specimen of I 7; longitudinal section of anterior end; shows disintegration of cells in anterior part of intestine, cephalic ganglion in early stage, and tissue growing in between intestine and cephalic ganglion;  $\times 400$ .
- Fig. 68.—Similar section of another specimen of the same lot;  $\times 400$ .
- Fig. 69.—Similar section of specimen from same lot;  $\times 400$ .





## PLATE VII



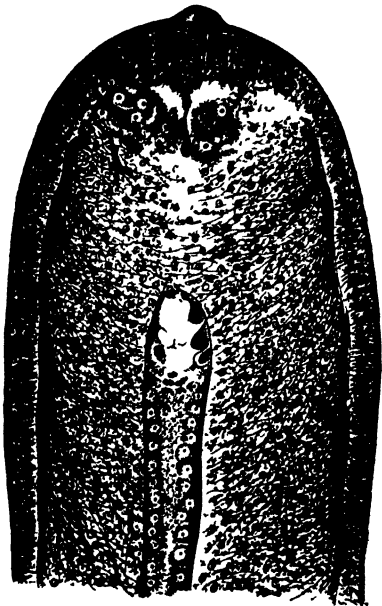
## EXPLANATION OF PLATE

*Gordius robustus*

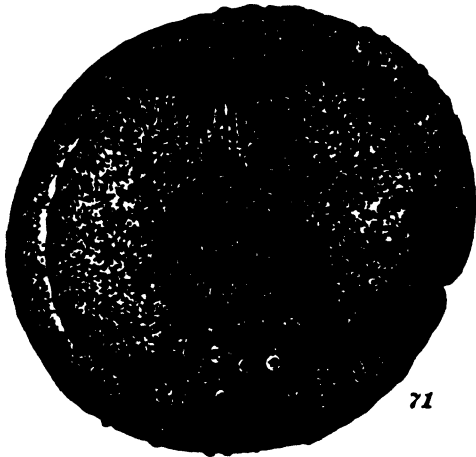
- Fig. 70.—Young male; section near posterior end; junction of intestine and sperm ducts;  $\times 380$ .
- Fig. 71.—Cross section posterior to that of Fig. 70;  $\times 380$ .
- Fig. 72.—Young male; same specimen as Fig. 29; section thru middle of body;  $\times 380$ .
- Fig. 73.—Anterior end of young specimen; longitudinal section; shows intestine ending considerably posterior to cephalic ganglion, remnants of proboscis, and cord connecting stylets with partition between body and proboscis;  $\times 220$ .
- Fig. 74.—Similar section of specimen almost fully developed;  $\times 105$ .



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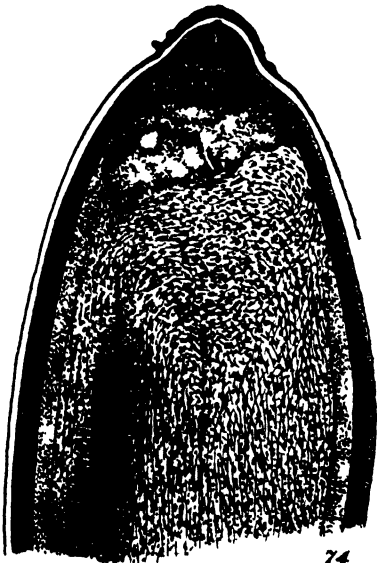
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**PLATE VIII**

## EXPLANATION OF PLATE

*Gordius robustus*

Fig. 75.—Cross section of male somewhat older than that of Fig. 72;  $\times$  195.

Fig. 76.—Cross section thru young female of about the same age;  $\times$  195.

Fig. 77.—Cross section thru female with adult cuticula nearly complete;  $\times$  60.

Fig. 78.—Sagittal section thru posterior end of female, nearly adult;  $\times$  55.

Fig. 79.—Female at beginning of formation of adult cuticula; cross section near anterior end of body;  $\times$  130.

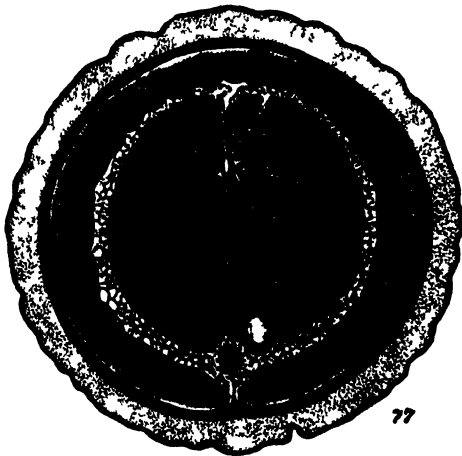
Fig. 80.—Cross section of male in same stage of development as female of Fig. 77;  $\times$  80.



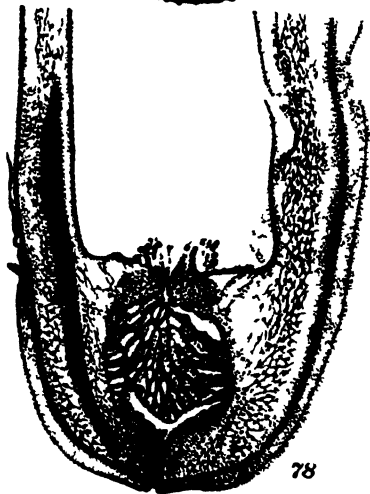
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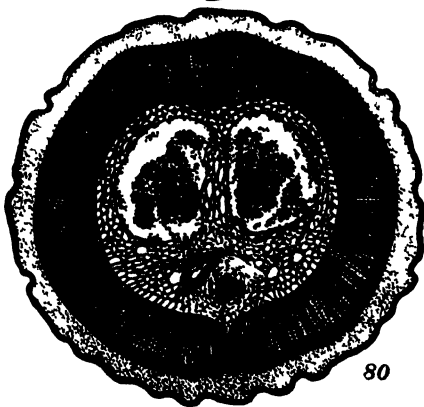
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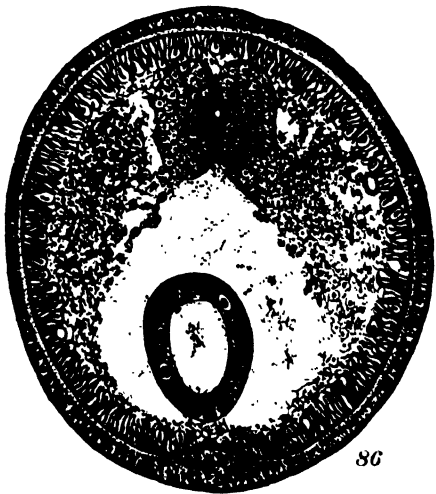
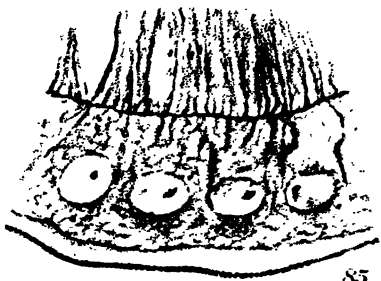
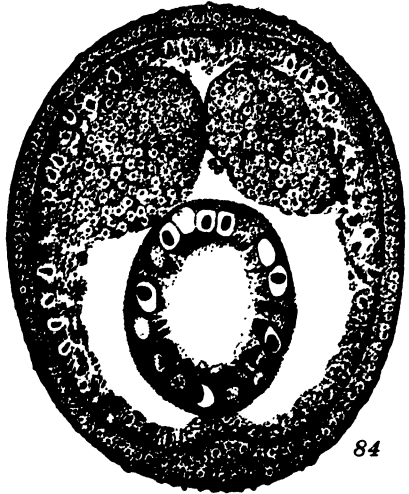
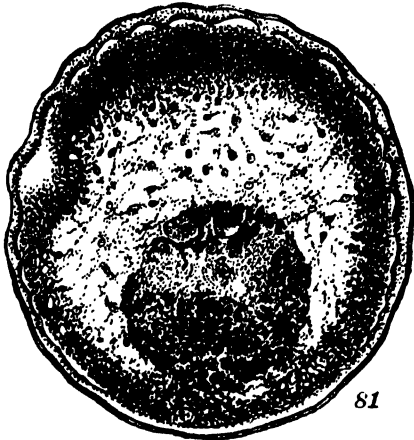
## PLATE IX



## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 81.—Cross section thru cephalic ganglion just before formation of adult cuticula; early large cells near middle of section;  $\times 160$ .
- Fig. 82.—Adjacent section just posterior to that of Fig. 81;  $\times 160$ .
- Fig. 83.—Adjacent section posterior to that of Fig. 82;  $\times 160$ .
- Fig. 84.—Young female; buds forming on ovarian tubes;  $\times 270$ .
- Fig. 85.—Early stage in development of adult cuticula; formation of hyaline layer outside of adult cuticula;  $\times 640$ .
- Fig. 86.—Young female; cross section showing early growth period in oocytes;  $\times 170$ .



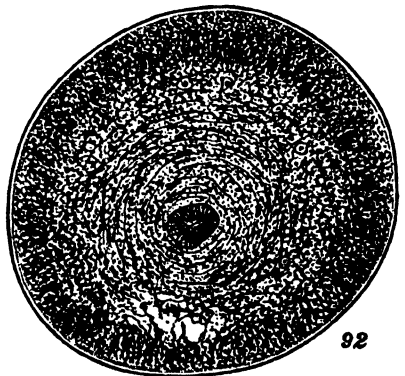
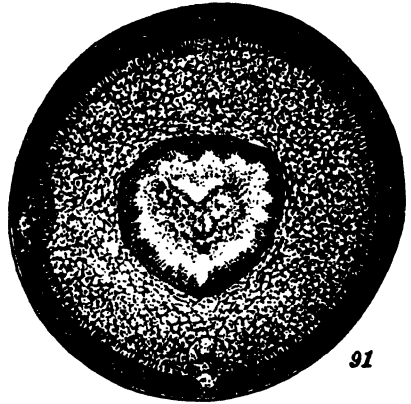


## PLATE X

## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 87.—Female at beginning of formation of adult cuticula; cross section near middle of body;  $\times 95$ .
- Fig. 88.—Section near posterior end of same female; seminal receptacle and ovaries just before they pass over into the oviducts;  $\times 105$ .
- Fig. 89.—Section slightly posterior to that of Fig. 88;  $\times 105$ .
- Fig. 90.—Section slightly posterior to that of Fig. 89;  $\times 105$ .
- Fig. 91.—Section thru posterior end of cloacal gland of same female;  $\times 105$ .
- Fig. 92.—Section behind cloacal gland of same female; cloacal ganglion;  $\times 140$ .





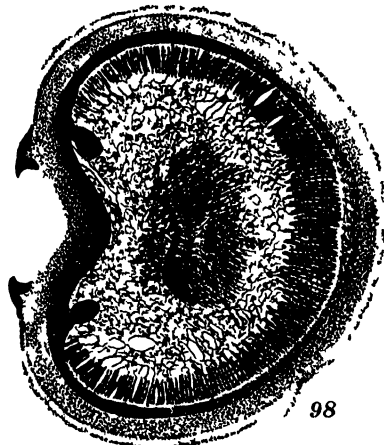
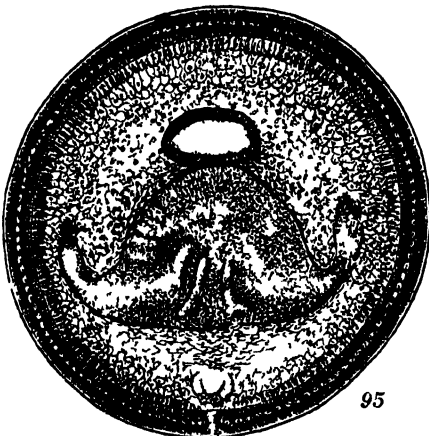
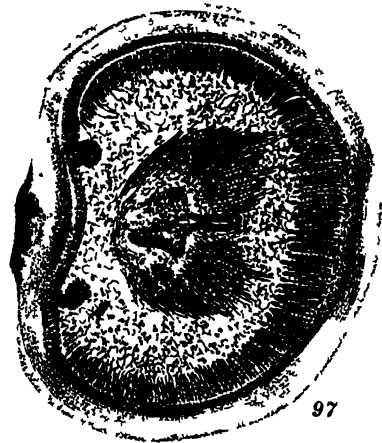
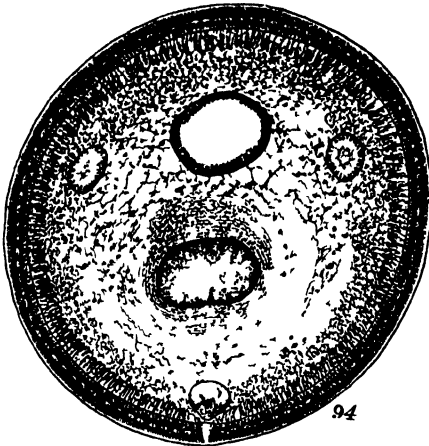
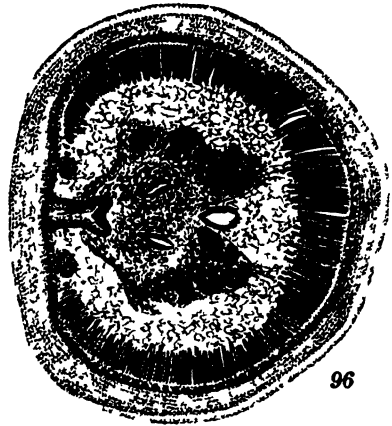
## PLATE XI



## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 93.—Section thru anterior end of cloacal gland of female shown in Plate 10; oviducts, intestine, and posterior end of seminal receptacle;  $\times 105$ .
- Fig. 94.—Section thru constriction between cloacal gland and seminal receptacle; circular musculature surrounding constriction;  $\times 105$ .
- Fig. 95.—Section posterior to that of Fig. 94; entrance of oviducts into cloaca;  $\times 105$ .
- Fig. 96.—Cross section thru cloacal musculature of male, nearly adult; just behind anus;  $\times 90$ .
- Fig. 97.—Section a short distance behind that of Fig. 96;  $\times 90$ .
- Fig. 98.—Section thru crescent of same male;  $\times 90$ .

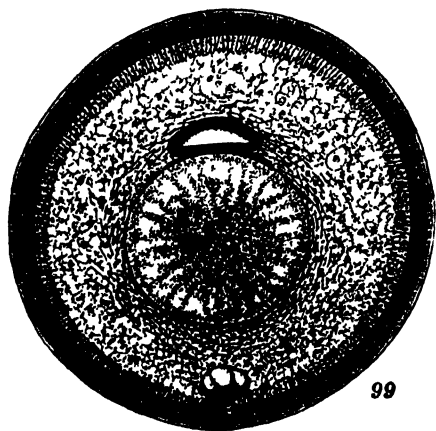




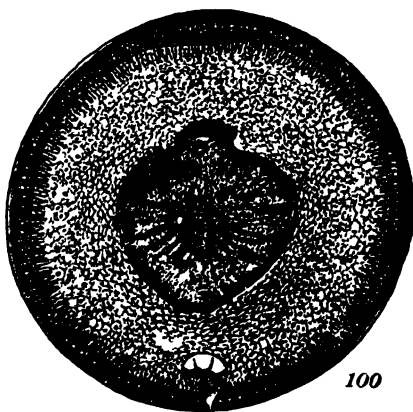
## PLATE XII

## EXPLANATION OF PLATE

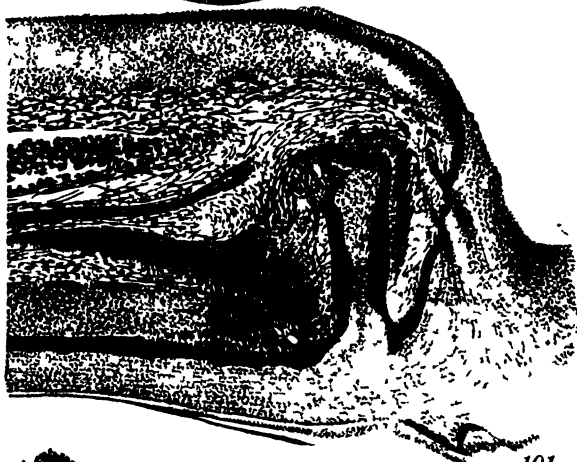
- Fig. 99.—*Gordius robustus*, section thru cloacal ganglion of same female as Fig. 95;  $\times$  105.
- Fig. 100.—*G. robustus*, section slightly posterior to that of Fig. 99; intestine enters cloaca;  $\times$  105.
- Fig. 101.—*G. robustus*, sagittal section thru cloacal ganglion of male; crescent in process of formation;  $\times$  105.
- Fig. 102.—*G. robustus*, same section as Fig. 101;  $\times$  340.
- Fig. 103.—*Paragordius varius*, cross section thru female that has deposited its eggs;  $\times$  70.
- Fig. 104.—*P. varius*, tangential section thru developing adult cuticula; areolae in the process of formation;  $\times$  400.



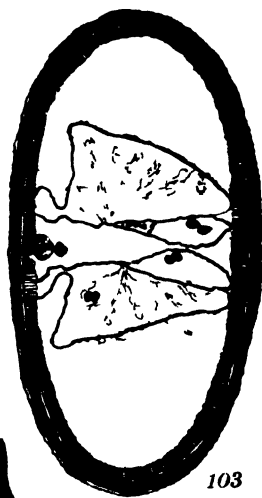
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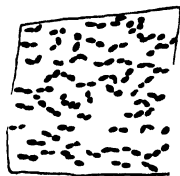
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## PLATE XIII



## EXPLANATION OF PLATE

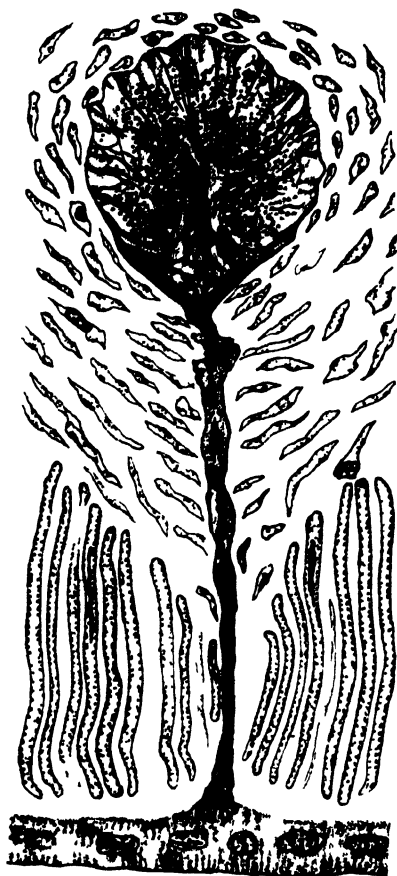
*Gordius robustus*

Fig. 105.—Cross section of nerve cord of adult;  $\times 700$ .

Fig. 106.—Nerve cord in specimen with adult cuticula nearly complete;  $\times 340$ .

Fig. 107.—Section near posterior end of male with fibrous cuticula nearly complete;  $\times 120$ .

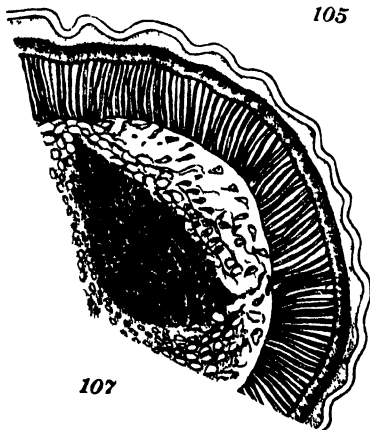
Fig. 108.—Section thru anterior end of same specimen as Fig. 107;  $\times 120$ .



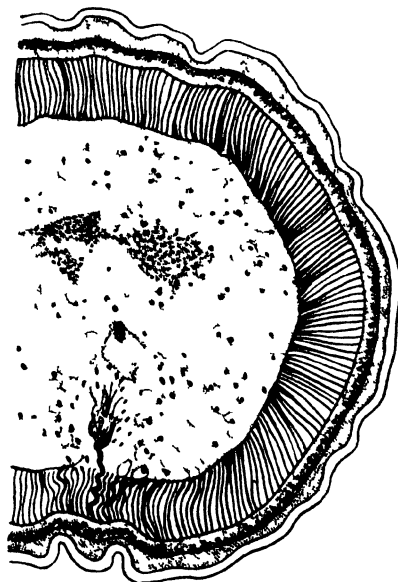
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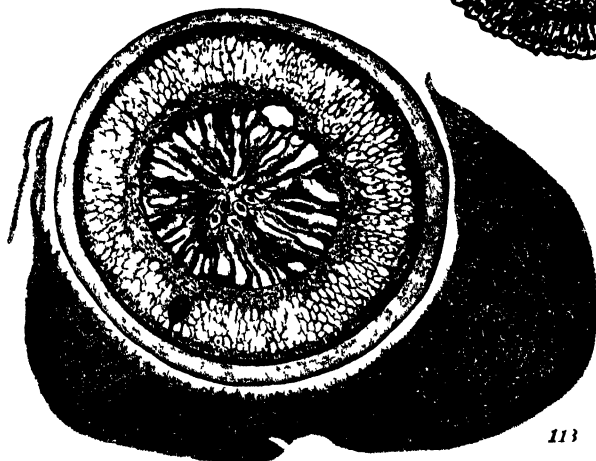
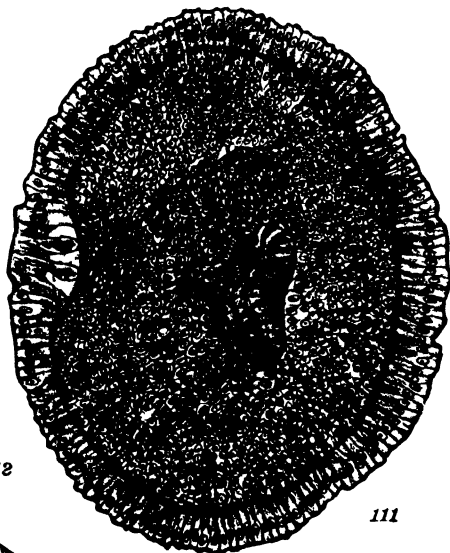
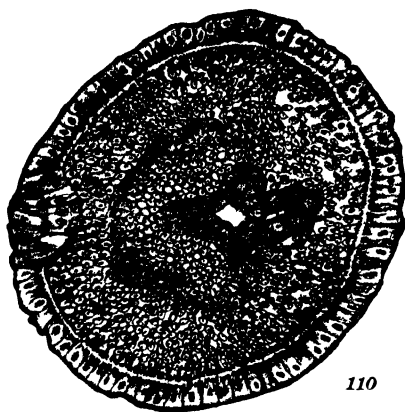


## PLATE XIV

## EXPLANATION OF PLATE

*Gordius robustus*

- Fig. 109.—Young female; cross section near posterior end; early stages of oviducts, seminal receptacle, and cloacal gland;  $\times 250$ .
- Fig. 110.—Section slightly posterior to that of Fig. 109;  $\times 250$ .
- Fig. 111.—Section thru posterior end of cloacal gland of same female;  $\times 250$ .
- Fig. 112.—Development of cuticula and muscles; slightly later stage than Fig. 85;  $\times 720$ .
- Fig. 113.—Cross section thru posterior region of female showing mass of spermatozoa adhering to outside;  $\times 60$ .
- Fig. 114.—Cross section of nerve cord of adult;  $\times 530$ .





## PLATE XV



## EXPLANATION OF PLATE

*Gordius robustus*

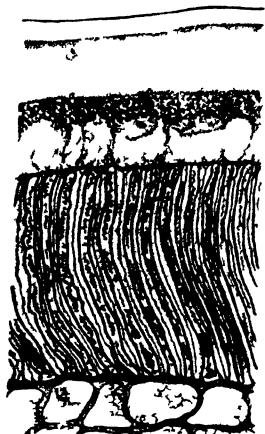
- Fig. 115.—Nerve fibre entering hypoderm of adult;  $\times 475$ .  
Fig. 116.—Early stage in development of fibrous cuticula; slightly later stage than Fig. 35;  $\times 800$ .  
Fig. 117.—Fibrous cuticula about half developed;  $\times 430$ .  
Fig. 118.—Adult; nerve fibres passing from neural lamella into hypoderm;  $\times 450$ .  
Fig. 119.—Fibrous cuticula; development almost complete;  $\times 625$ .  
Fig. 120.—Nerve fibres in hypoderm of adult;  $\times 435$ .  
Fig. 121.—Cross section thru inner, ventral wall of prong of male; shows stout bristle;  $\times 625$ .  
Fig. 122.—Section slightly outward from that of Fig. 121;  $\times 625$ .  
Fig. 123.—Section thru outer wall of prong of same specimen;  $\times 625$ .  
Fig. 124.—Old specimen; section showing extreme degeneration of muscles;  $\times 430$ .  
Fig. 125.—Section thru old specimen; shows beginning of degeneration of muscle fibres;  $\times 430$ .  
Fig. 126.—End of muscle cell of adult; isolated after maceration with nitric acid;  $\times 625$ .



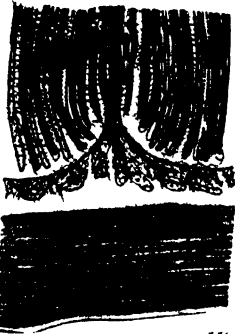
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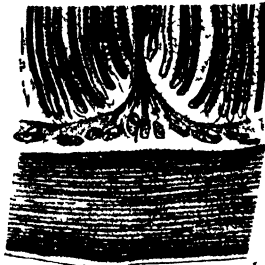
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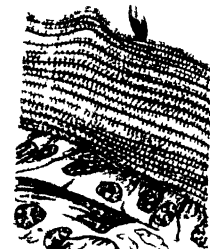
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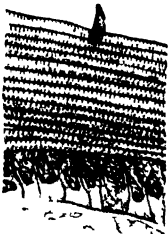
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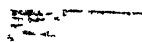
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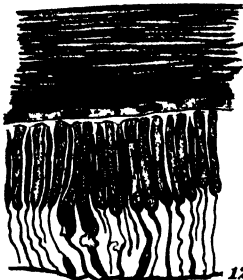
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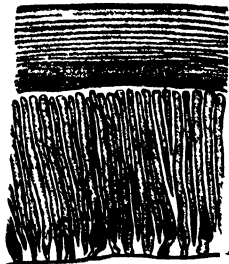
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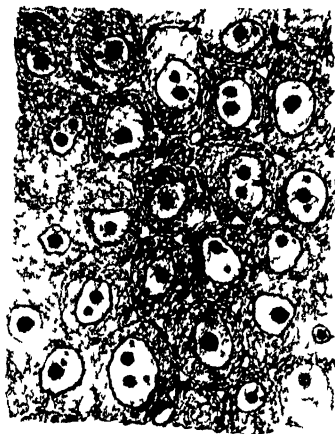
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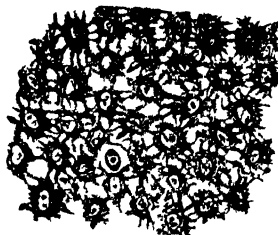
## PLATE XVI

## EXPLANATION OF PLATE

- Fig. 127.—*Gordius robustus*, tangential section of hypoderm of young specimen; shows nuclei and nucleoli as well as radiating canals;  $\times 800$ .
- Fig. 128.—*G. robustus*, tangential section thru hypoderm of specimen in which fibrous cuticula is forming; intercellular bridges;  $\times 400$ .
- Fig. 129.—*G. robustus*, section similar to that of Fig. 128; nerve fibre in hypoderm;  $\times 475$ .
- Fig. 130.—*Paragordius varius*, young parasite in the coiled stage;  $\times 190$ .
- Fig. 131.—*P. varius*, very young parasite; side view; specimen somewhat flattened;  $\times 250$ .
- Fig. 132.—*P. varius*, anterior end of adult; side view; semi-transparent;  $\times 70$ .
- Fig. 133.—*P. varius*, posterior end of adult male; ventral view, shows rows of bristles;  $\times 70$ .
- Fig. 134.—*P. varius*, cross section of host containing young parasite;  $\times 37$ .
- Fig. 135.—*P. varius*, section of parasite from Fig. 134;  $\times 130$ .
- Fig. 136.—*P. varius*, cross section thru middle of body of young specimen; early development of gonads;  $\times 500$ .
- Fig. 137.—*P. varius*, spermatozoa; smear made from male;  $\times 800$ .
- Fig. 138.—*P. varius*, spermatozoa; smear made from seminal receptacle of female;  $\times 800$ .
- Fig. 139.—*P. varius*, longitudinal section parallel to large nerve cells in ventral cord; shows bipolar cells;  $\times 250$ .



127



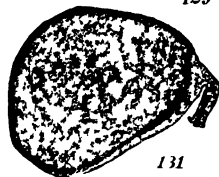
128



129



130



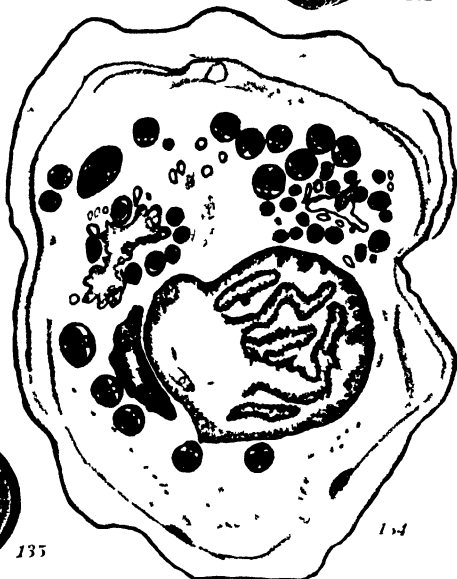
131



132



133



134



135



136



137



138



139



## PLATE XVII



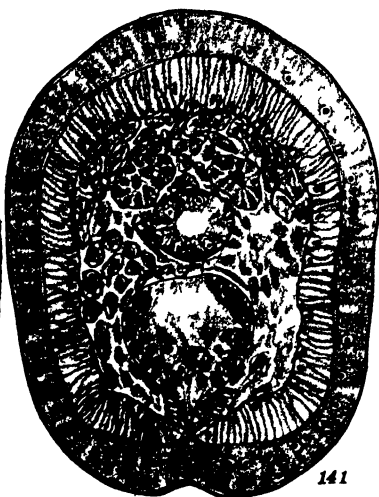
## EXPLANATION OF PLATE

*Paragordius varius*

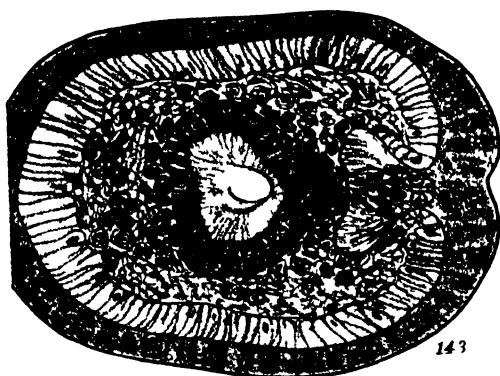
- Fig. 140.—Cross section thru posterior end of male at time of formation of adult cuticula;  $\times$  365.
- Fig. 141.—Section thru posterior region of young male;  $\times$  375.
- Fig. 142.—Section of same specimen; shows sperm ducts entering cloaca;  $\times$  375.
- Fig. 143.—Section thru cloaca of same specimen;  $\times$  375.
- Fig. 144.—Section thru same specimen at base of prongs;  $\times$  375.
- Fig. 145.—Young parasite; cross section;  $\times$  500.



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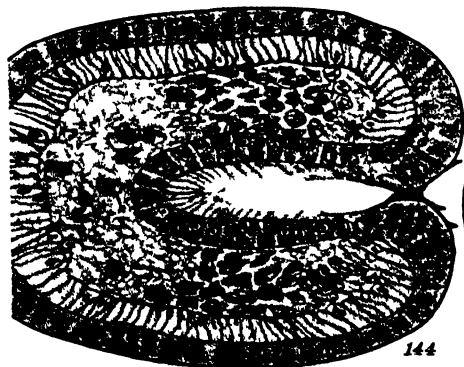
141



143



142



144



145

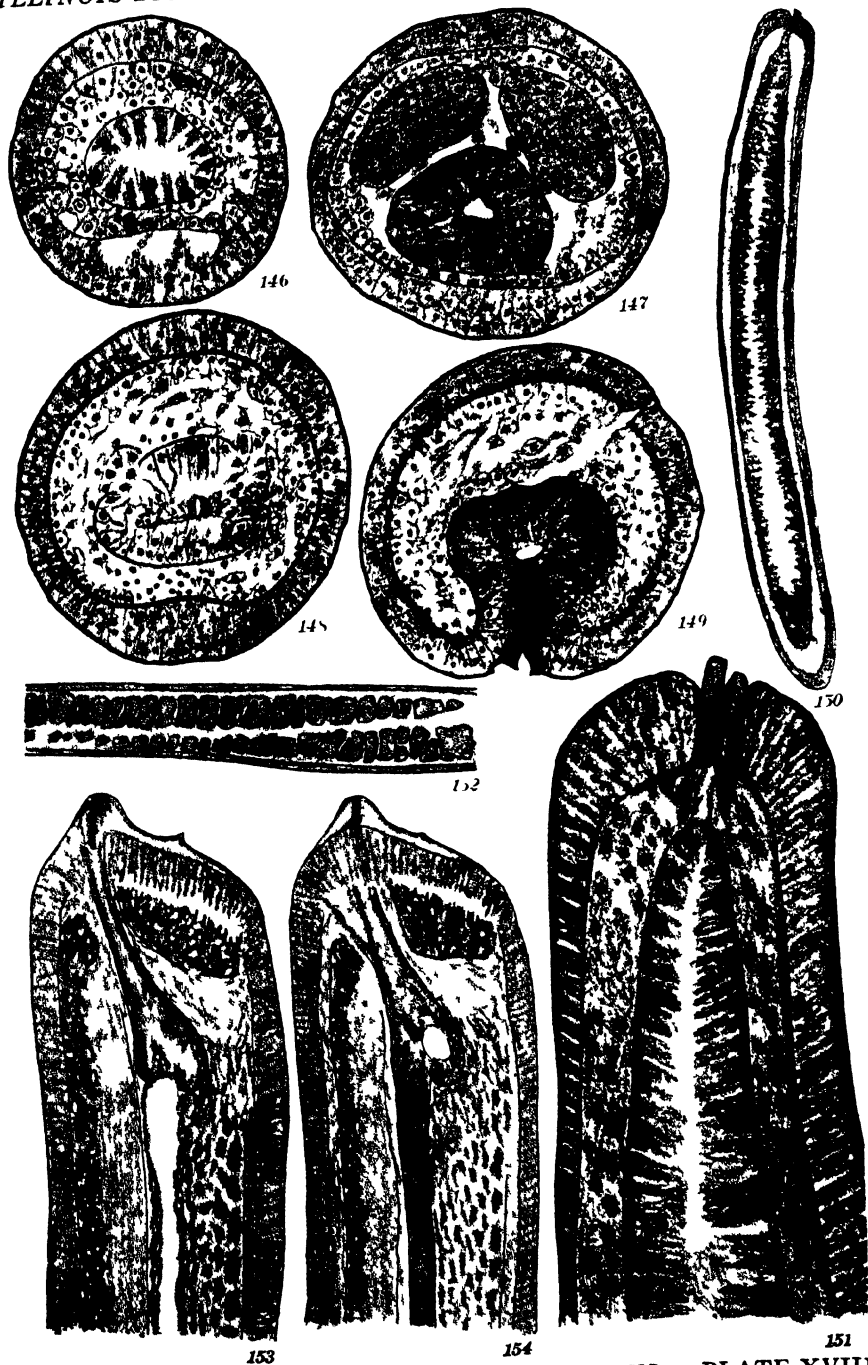


## PLATE XVIII

## EXPLANATION OF PLATE

*Paragordius varius*

- Fig. 146.—Cross section near anterior end of young specimen;  $\times 500$ .  
Fig. 147.—Section near middle of body of same specimen;  $\times 500$ .  
Fig. 148.—Section near posterior end of young male; intestinal diverticula for entrance of sperm ducts;  $\times 500$ .  
Fig. 149.—Section thru anal region of same male;  $\times 500$ .  
Fig. 150.—Young specimen; longitudinal section thru anterior end;  $\times 115$ .  
Fig. 151.—Part of Fig. 150; shows connection between intestine and proboscis;  $\times 500$ .  
Fig. 152.—Longitudinal section thru anterior region of female; shows ovarian pockets which appear to be placed irregularly not indicating segmentation;  $\times 25$ .  
Fig. 153.—Sagittal section thru anterior end of young specimen; shows esophagus;  $\times 150$ .  
Fig. 154.—Section adjacent to that of Fig. 153;  $\times 150$ .



MAY

GORDIUS AND PARAGORDIUS

PLATE XVIII



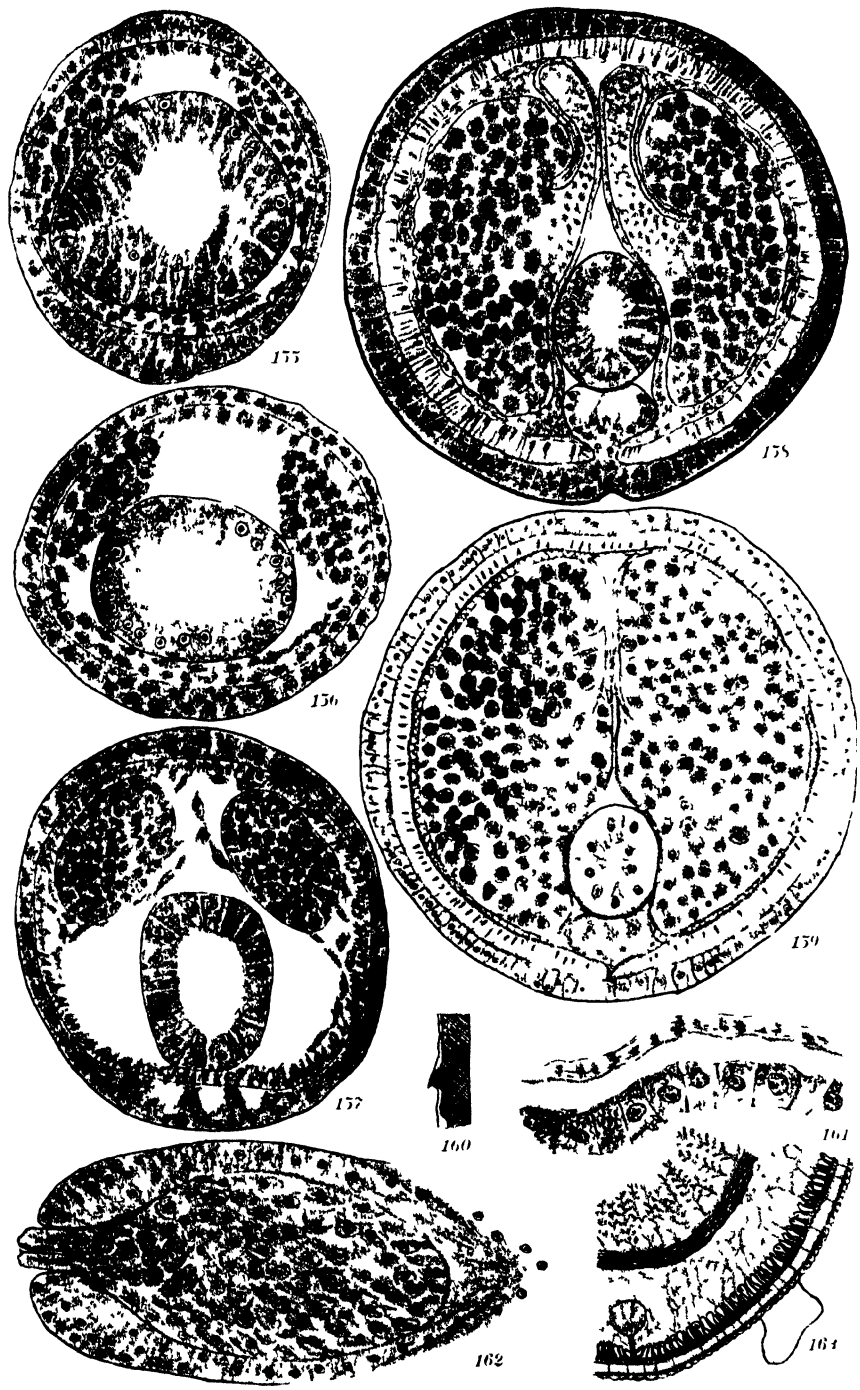
## PLATE XIX



## EXPLANATION OF PLATE

*Paragordius varius*

- Fig. 155.—Section thru young parasite;  $\times 500$ .  
Fig. 156.—Section near middle of body of young parasite;  $\times 500$ .  
Fig. 157.—Section near middle of body of slightly older parasite;  $\times 500$ .  
Fig. 158.—Section thru middle of body of young female; just before formation of adult cuticula; shows formation of mesenteries;  $\times 400$ .  
Fig. 159.—Section thru female at beginning of formation of adult cuticula; mesenteries formed;  $\times 200$ .  
Fig. 160.—Longitudinal section thru cuticula; shows areola and protoplasmic strand;  $\times 400$ .  
Fig. 161.—Ventral part of female during formation of adult cuticula; cross section; formation of areolae;  $\times 500$ .  
Fig. 162.—Slightly oblique section thru anterior end of young parasite; beginning of cephalic ganglion;  $\times 500$ .  
Fig. 163.—Cross section thru cloacal gland of female at the time the larval cuticula is shed; larval cuticula partly loose;  $\times 150$ .



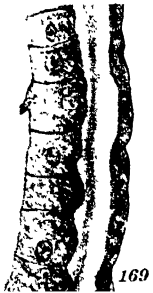
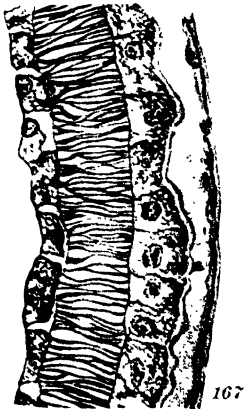
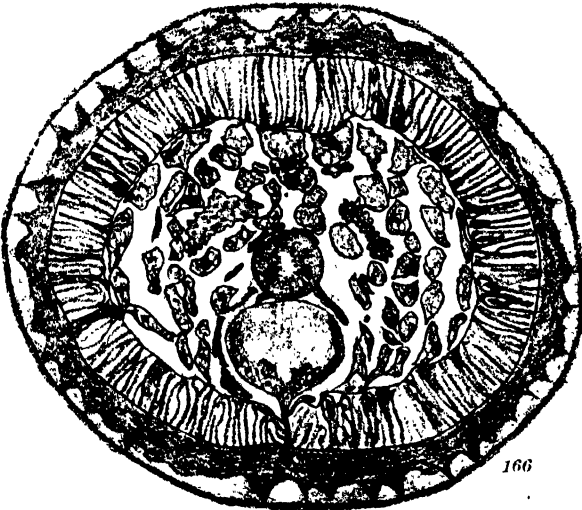
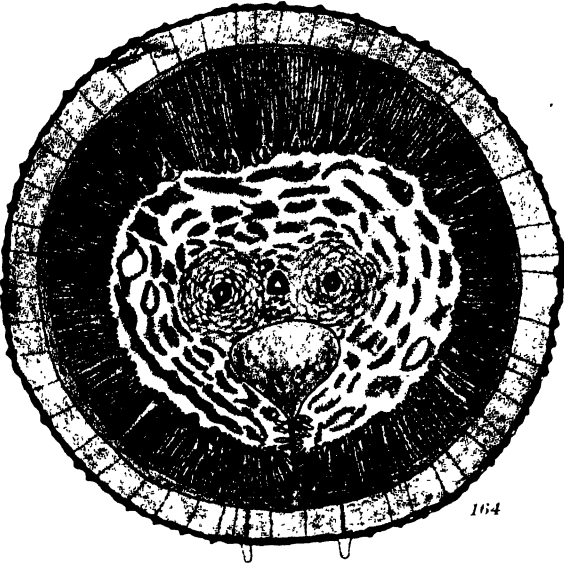


## PLATE XX

## EXPLANATION OF PLATE

*Paragordius varius*

- Fig. 164.—Section thru posterior end of adult male; cloacal ganglion and circular muscles surrounding the sperm ducts;  $\times 275$ .
- Fig. 165.—Longitudinal section thru posterior end of young parasite; shows invaginated ectoderm forming intestinal diverticula;  $\times 500$ .
- Fig. 166.—Cross section thru anterior region of specimen with adult cuticula nearly complete; shows cellular projections into cuticula;  $\times 275$ .
- Fig. 167.—Cross section of female with adult cuticula nearly formed; cellular projections and formation of areolae;  $\times 500$ .
- Fig. 168.—Sagittal section thru upper end of cloaca of female;  $\times 100$ .
- Fig. 169.—Early stage in formation of cuticula; areolae very small;  $\times 500$ .





## PLATE XXI



## EXPLANATION OF PLATE

*Paragordius varius*

Fig. 170.—Cross section thru body of young female; ovarian buds not yet formed;  $\times 500$ .

Fig. 171.—Frontal section thru upper end of cloaca of young female;  $\times 115$ .

Fig. 172.—Cross section thru body of female; dorsal part of section; beginning of formation of adult cuticula; structure of dorsal part of mesenteries;  $\times 500$ .

Fig. 173.—Ventral part of same section as Fig. 172;  $\times 500$ .

Fig. 174.—Cross section of male at beginning of formation of adult cuticula;  $\times 375$ .



MAY

GORDIUS AND PARAGORDIUS

PLATE XXI



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# STUDIES ON MYXOSPORIDIA

A SYNOPSIS OF GENERA AND SPECIES  
OF MYXOSPORIDIA

WITH 25 PLATES AND 2 TEXTFIGURES

BY  
ROKUSABURO KUDO

Contributions from the  
Zoological Laboratory of the University of Illinois  
No. 158



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## INTRODUCTION

Ten years have elapsed since Auerbach (1910) published *Die Cnidosporidien* in which he gave a synopsis of the genera and species of Myxosporidia known up to that time. During this period new genera and a number of new species have been added to the list of this particular group of parasitic protozoa from the various parts of the world. It is, therefore, desirable to have a complete monographic work including all the forms reported up to the present time.

The main objects of the present paper are: 1) to describe a new genus and a number of new species which have come under the observation of the writer; 2) to collect all the genera and species recorded by various authors; 3) to propose a new classification by which some of the confusion now existing may, probably, be avoided; 4) to show the geographical, zoological and organal distribution in the light of more recent observations; and 5) to present a complete list of the names of the hosts in which Myxosporidia occur.

The writer believes himself to be in possession of as complete references as possible under present conditions. However, he may be unaware of some works which have not reached him owing to the war.

The Myxosporidia recorded by Labbé (1899) are arranged in almost the same order as that author listed them, with some slight change such as placing the type species at the front of each genus or removing a few species to other genera, while those species which have been described since 1898 are arranged chronologically, no matter whether names are given the species or not.

Some of the references are omitted, especially when they can be found in Gurley (1894), Thélohan (1895), Labbé (1899), or Auerbach (1910). The description of each species is given according to the first observer. The observations of subsequent investigators are then mentioned in the second place.

Each species is described according to the following scheme:

- 1) Specific name
- 2) Synonyms and literature
- 3) Habitat, including the locality and the date of observation
- 4) Vegetative form
- 5) Spore
- 6) Remarks

I wish to express my appreciation to Professor Henry B. Ward whose kindness has made the completion of this paper possible.

### GENERAL REMARKS ON RECENT OBSERVATIONS

The total number of species of Myxosporidia reported up to date and described in the following pages, excluding 12 ambiguous forms, reaches 237 of which 125 are species which have been observed since 1910.\*

The distribution of these new forms is as follows:

Africa.....	6 species
Asia .. ...	23 species
Australia... ..	1 species
Europe. . ...	31 species
North America. . .	63 species
South America	1 species

Thus, the majority of the species were observed in other lands than Europe, nearly half being recorded from North American waters. It is not hard to anticipate from the observations made by Awerinzew, Davis, Kudo, Mavor, Johnston and Bancroft, and others, that further investigations on the parasites in the localities where the study of the protozoa under consideration was neglected, will bring out not only new and interesting forms which will be quite different from the comparatively well studied European species, but also many important facts that will clear unknown or doubtful phases concerning the life history and structure of Myxosporidia.

\* Three species are included here which have been described (in Nipponese) by Miyairi in 1909.

## MYXOSPORIDIA RECORDED IN THE PRESENT PAPER

## LIST I

## Order MYXOSPORIDIA Bütschli

## I Suborder EURYSPOREA nom. nov. (see page 56)

## I Family CERATOMYXIDAE Doflein

## Genus 1 LEPTOTHECA Thélohan

[15 species]

- 1) *L. agilis* Thélohan (type species)
- 2) *L. elongata* Thélohan
- 3) *L. polymorpha* (Thél.) Labbé
- 4) *L. parva* Thélohan
- 5) *L. renicola* Thélohan
- 6) *L. hepseli* Thélohan
- 7) *L. perlata* (Gurley) Labbé
- 8) *L. sp.* Awerinzew
- 9) *L. macrospora* Auerbach
- 10) *L. informis* Auerbach
- 11) *L. longipes* Auerbach
- 12) *L. fusiformis* Davis
- 13) *L. scissura* Davis
- 14) *L. lobosa* Davis
- 15) *L. glomerata* Davis

## Genus 2 CERATOMYXA Thélohan

[35 species]

- 1) *C. arcuata* Thélohan (type species)
- 2) *C. sphaerulosa* Thélohan
- 3) *C. pallida* Thélohan
- 4) *C. globulifera* Thélohan
- 5) *C. appendiculata* Thélohan
- 6) *C. truncata* Thélohan
- 7) *C. reticularis* Thélohan
- 8) *C. inaequalis* Doflein
- 9) *C. linosporea* Doflein
- 10) *C. ramosa* Awerinzew
- 11) *C. drepanopsellae* Awerinzew
- 12) *C. tylosuri* Awerinzew
- 13) *C. (?) spari* Awerinzew
- 14) *C. sp. (?)* Awerinzew
- 15) *C. sp. (?)* Awerinzew
- 16) *C. acadiensis* Mavor

17) *C. sp.* Georgévitch18) *C. coris* Georgévitch19) *C. herouardi* Georgévitch20) *C. mesospora* Davis21) *C. sphairophora* Davis22) *C. taenia* Davis23) *C. attenuata* Davis24) *C. recurvata* Davis25) *C. lunata* Davis26) *C. abbreviata* Davis27) *C. flagellifera* Davis28) *C. agglomerata* Davis29) *C. amorphia* Davis30) *C. monospora* Davis31) *C. streptospora* Davis32) *C. aggregata* Davis33) *C. undulata* Davis34) *C. navicularia* Davis35) *C. spinosa* Davis

## Genus 3 MYXOPROTEUS Doflein

[3 species]

1) *M. ambiguus* (Thélohan) Doflein (type species)2) *M. cordiformis* Davis3) *M. cornutus* Davis

## Genus 4 WARDIA nov. gen.

[2 species]

1) *W. ovinocua* nov. spec. (type species)2) *W. ohlmacheri* (Gurley) Kudo

## Genus 5 MITRASPOREA Fujita emend.

Kudo [3 species]

1) *M. cyprini* Fujita (type species)2) *M. caudata* (Parisi) Kudo3) *M. elongata* nov. spec.

## II Suborder SPHAEROSPOREA nom. nov. (see page 57)

## I Family CHLOROMYXIDAE Thélohan

- Genus 1 CHLOROMYXUM Mingazzini [22 species]
- |  |                                    |
|--|------------------------------------|
| 1) <i>C. leydi</i> Mingazzini (type species) | 11) <i>C. sp.</i> Awerinzew        |
| 2) <i>C. caudatum</i> Thélohan               | 12) <i>C. thymalli</i> Lebselter   |
| 3) <i>C. quadratum</i> Thélohan              | 13) <i>C. koi</i> Fujita           |
| 4) <i>C. fluviatile</i> Thélohan             | 14) <i>C. magnum</i> Awerinzew     |
| 5) <i>C. mucronatum</i> Gurley               | 15) <i>C. funduli</i> Hahn         |
| 6) <i>C. diploxy</i> (Gurley) Thélohan       | 16) <i>C. misgurni</i> Kudo        |
| 7) <i>C. protei</i> Joseph                   | 17) <i>C. fujitai</i> Kudo         |
| 8) <i>C. truttiae</i> Léger                  | 18) <i>C. clupeidae</i> Hahn       |
| 9) <i>C. cristatum</i> Léger                 | 19) <i>C. granulorum</i> Davis     |
| 10) <i>C. dubium</i> Auerbach                | 20) <i>C. trijugum</i> nov. spec.  |
|  | 21) <i>C. calostomi</i> nov. spec. |
|  | 22) <i>C. wardi</i> nov. spec.     |

## II Family SPHAEROSPORIDAE Davis

- Genus 1 SPHAEROSPORA Thélohan [10 species]
- |  |  |
|--|--|
| 1) <i>S. divergens</i> Thélohan (type species) | 9) <i>S. (?) sp.</i> Southwell et Prashad  |
| 2) <i>S. elegans</i> Thélohan                  | 10) <i>S. carassii</i> nov. spec.          |
| 3) <i>S. rostrata</i> Thélohan                 |  |
| 4) <i>S. masovica</i> Cohn                     | Genus 2 SINUOLINEA Davis [5 species]       |
| 5) <i>S. platessae</i> Woodcock                | 1) <i>S. dimorpha</i> Davis (type species) |
| 6) <i>S. angulata</i> Fujita                   | 2) <i>S. capsularis</i> Davis              |
| 7) <i>S. sp.</i> Davis                         | 3) <i>S. arborescens</i> Davis             |
| 8) <i>S. polymorpha</i> Davis                  | 4) <i>S. opacita</i> Davis                 |
|  | 5) <i>S. brachiophora</i> Davis            |

## III Suborder PLATYSPOREA nom. nov. (see page 57)

## I Family MYXIDIIDAE Thélohan

- Genus 1 MYXIDIUM Bütschli [26 species]
- |  |  |
|--|--|
| 1) <i>M. lieberkühni</i> Bütschli (type species) | 21) <i>M. gadi</i> Georgévitch                 |
| 2) <i>M. incurvatum</i> Thélohan                 | 22) <i>M. glutinosum</i> Davis                 |
| 3) <i>M. sphaericum</i> Thélohan                 | 23) <i>M. phyllium</i> Davis                   |
| 4) <i>M. histophilum</i> Thélohan                | 24) <i>M. striatum</i> Cunha et Fonseca        |
| 5) <i>M. sp.</i> Gurley                          | 25) <i>M. kagayamai</i> nov. spec.             |
| 6) <i>M. danilewskyi</i> Laveran                 | 26) <i>M. americanum</i> nov. spec.            |
| 7) <i>M. giganteum</i> Doflein                   |  |
| 8) <i>M. barbatulae</i> Cépède                   | Genus 2 SPHAEROMYXA Thélohan [7 species]       |
| 9) <i>M. giardi</i> Cépède                       | 1) <i>S. balbianii</i> Thélohan (type species) |
| 10) <i>M. pfeifferi</i> Auerbach                 | 2) <i>S. immersa</i> (Lutz) Thélohan           |
| 11) <i>M. inflatum</i> Auerbach                  | 3) <i>S. incurvata</i> Doflein                 |
| 12) <i>M. bergense</i> Auerbach                  | 4) <i>S. sabraesi</i> Laveran et Mesnil        |
| 13) <i>M. procerum</i> Auerbach                  | 5) <i>S. hellandi</i> Auerbach                 |
| 14) <i>M. mackiei</i> Bosanquet                  | 6) <i>S. exneri</i> Awerinzew                  |
| 15) <i>M. macrocapsulare</i> Auerbach            | 7) <i>S. gasterostei</i> Georgévitch           |
| 16) <i>M. sp.</i> Awerinzew                      |  |
| 17) <i>M. depressum</i> Parisi                   | Genus 3 ZSCHOKKELLA Auerbach [4 species]       |
| 18) <i>M. oviforme</i> Parisi                    | 1) <i>Z. hildae</i> Auerbach (type species)    |
| 19) <i>M. anguillae</i> Ishii                    | 2) <i>Z. nova</i> Klokacewa                    |
| 20) <i>M. sp.</i> Mavor                          | 3) <i>Z. acheilognathi</i> Kudo                |
|  | 4) <i>Z. globulosa</i> Davis                   |

## II Family MYXOSOMATIDAE Poche

Genus 1 MYXOSOMA Thélohan  
[3 species]

- 1) *M. dujardini* Thélohan (type species)
- 2) *M. (?) lobatum* Nemeček
- 3) *M. funduli* Kudo

Genus 2 LENTOSPORA Plehn  
[6 species]

- 1) *L. cerebralis* (Hofer) Plehn (type species)
- 2) *L. multiplicata* Reuss
- 3) *L. encephalina* Mulsow
- 4) *L. asymmetrica* Parisi
- 5) *L. acuta* (Fujita) Kudo
- 6) *L. dermatobia* Ishii

## III Family MYXOBOLIDAE Thélohan

Genus 1 MYXOBOLUS Bütschli  
[63 species]

- 1) *M. mulleri* Bütschli (type species)
- 2) *M. piriformis* Thélohan
- 3) *M. unicapsulatus* Gurley
- 4) *M. fuhrmanni* Auerbach
- 5) *M. oculi-leucisci* Trojan
- 6) *M. toyamai* Kudo
- 7) *M. notatus* Mavor
- 8) *M. sp.* Kudo
- 9) *M. rohithae* Southwell et Prashad
- 10) *M. seni* Southwell et Prashad
- 11) *M. misgurni* nov. spec.
- 12) *M. pfeifferi* Thélohan
- 13) *M. inaequalis* Gurley
- 14) *M. dispar* Thélohan
- 15) *M. ellipsoides* Thélohan
- 16) *M. exiguus* Thélohan
- 17) *M. oviformis* Thélohan
- 18) *M. lintoni* Gurley
- 19) *M. globosus* Gurley
- 20) *M. oblongus* Gurley
- 21) *M. transovalis* Gurley
- 22) *M. obesus* Gurley
- 23) *M. cycloides* Gurley
- 24) *M. sphaeralis* Gurley
- 25) *M. anurus* Cohn
- 26) *M. sp.* Gurley
- 27) *M. sp.* Gurley
- 28) *M. sp.* Gurley
- 29) *M. cyprini* Doflein
- 30) *M. neurobius* Schuberg et Schröder
- 31) *M. aeglefini* Auerbach
- 32) *M. gigas* Auerbach
- 33) *M. wolgensis* Reuss
- 34) *M. scardinii* Reuss
- 35) *M. physophilus* Reuss
- 36) *M. macrocapsularis* Reuss
- 37) *M. sandrae* Reuss
- 38) *M. bramae* Reuss

- 39) *M. cyprinicola* Reuss
- 40) *M. balleri* Reuss
- 41) *M. squamiae* Keysselitz
- 42) *M. cordis* Keysselitz
- 43) *M. musculi* Keysselitz
- 44) *M. sp.* Miyairi
- 45) *M. sp.* Wegener
- 46) *M. permagnus* Wegener
- 47) *M. rotundus* Nemeček
- 48) *M. minutus* Nemeček
- 49) *M. sp.* Lebzelter
- 50) *M. magnus* Awerinzew
- 51) *M. carassii* Klokacewa
- 52) *M. sp.* Southwell
- 53) *M. funduli* Kudo
- 54) *M. pleuronectidae* (Hahn)
- 55) *M. capsulatus* Davis
- 56) *M. nodularis* Southwell et Prashad
- 57) *M. hylae* Johnston et Bancroft
- 58) *M. aureatus* Ward
- 59) *M. miyairii* nov. spec.
- 60) *M. koi* nov. spec.
- 61) *M. orbiculatus* nov. spec.
- 62) *M. discrepans* nov. spec.
- 63) *M. mesentericus* nov. spec.

Genus 2 HENNEGUYA Thélohan  
[32 species]

- 1) *H. psorospermica* Thélohan (type species)
- 2) *H. texta* (Cohn) Labbé
- 3) *H. minuta* (Cohn) Labbé
- 4) *H. oviperda* (Cohn) Labbé
- 5) *H. lobosa* (Cohn) Labbé
- 6) *H. peri-intestinalis* Cépède
- 7) *H. media* Thélohan
- 8) *H. brevis* Thélohan
- 9) *H. schizura* (Gurley) Labbé
- 10) *H. creplini* (Gurley) Labbé

- 11) *H. linearis* (Gurley) Labbé
- 12) *H. gurleyi* Kudo
- 13) *H. strongylura* (Gurley) Labbé
- 14) *H. monura* (Gurley) Labbé
- 15) *H. kolesnikovii* (Gurley) Labbé
- 16) *H. macrura* (Gurley) Thélohan
- 17) *H. zschokkei* (Gurley) Doflein
- 18) *H. sp.* (Gurley) Labbé
- 19) *H. sp.* (Gurley) Labbé
- 20) *H. tenuis* Vaney et Conte
- 21) *H. nüsslini* Schuberg et Schröder
- 22) *H. legeri* Cépède
- 23) *H. acerinae* Schröder
- 24) *H. gigantea* Nemeček
- 25) *H. (?) sp.* Nemeček
- 26) *H. gasterostei* Parisi
- 27) *H. neapolitana* Parisi
- 28) *H. wisconsinensis* Mavor
- 29) *H. brachyura* Ward
- 30) *H. salminicola* Ward

- 31) *H. miyairii* nov. spec.
- 32) *H. mictospora* nov. spec.

Genus 3 HOFERELLUS Berg  
[1 species]

- 1) *H. cyprini* Doflein

Appendix: Myxosporidia of unknown genera  
and species [11 forms]

- 1) Gen. et spec. incert. Leydig
- 2) Gen. et spec. incert. Leydig
- 3) Gen. et spec. incert. Leydig
- 4) Gen. et spec. incert. Heckel et Kner
- 5) Gen. et spec. incert. Borne
- 6) Gen. incert. *merlucii* Perugia
- 7) Gen. incert. *congrui* Perugia
- 8) Gen. et spec. incert. Linton
- 9) Gen. et spec. incert. Mingazzini
- 10) Gen. et spec. incert. Nufer
- 11) Gen. et spec. incert. Mavor
- 12) Gen. et spec. incert. Mavor

## DISTRIBUTION OF MYXOSPORIDIA

## A. GEOGRAPHICAL DISTRIBUTION

As will be seen from List III, Myxosporidia are common parasites of fish in various parts of the world.

It is interesting to notice that the same species are found among fresh-water or marine fish from waters in widely separated countries. It is possible to think that Myxosporidia in marine fish may be carried into remote waters by the migration of their hosts, while those infecting fresh-water fish may be brought from one place to another by the transportation of infected fish for breeding purpose, etc. It should be noted in this connection that no intermediate host has yet been found in relation to myxosporidiosis.

The followings are the common species found in different localities:

<i>Leptotheca parva</i> Thél.	Marseille, Bergen
<i>Ceratomyxa sphaerulosa</i> Thél.	Monaco, Roscoff, Bergen
<i>C. appendiculata</i> Thél.	Roscoff, Marseille, Rovigno
<i>C. drepanopsellae</i> Awerinzew	Murman coast, Bergen, Woods Hole
<i>Chloromyxum leydigi</i> Ming.	Roscoff, Monaco, Napoli, Rovigno, Beaufort
<i>C. quadratum</i> Thél.	Roscoff, Marseille, Napoli, Beira
<i>Sphaerospora elegans</i> Thél.	Bretagne, Karlsruhe, Lago di Garda
<i>S. divergens</i> Thél.	Napoli, Roscoff, Smalfjorden
<i>Myxidium lieberkuhni</i> Bütsch.	Lago Maggiore, France, Germany, Lake Mendota, Georgian Bay
<i>M. incurvatum</i> Thél.	Napoli, Monaco, Roscoff, Bergen, Beaufort
<i>M. bergense</i> Auerbach.	Bergen, St. Andrews
<i>M. oviforme</i> Parisi	Napoli, Norwegian coast
<i>Sphaeromyxa balbianii</i> Thél.	Roscoff, Napoli, Beaufort
<i>Myxosoma dujardini</i> Thél.	France, Germany, Tokio(?)

On the other hand, some species are limited to certain localities. Five species classified in the genus *Sinuolinea* by Davis are reported only from Beaufort, N. C., U. S. A. The two species of the genus *Wardia* have been found solely in the state of Illinois, U. S. A.

More detailed data are shown in the following list.

## LIST II

## ASIA

## I NIPPON

Myxosporidia of fresh water fish

## 1) Northern Part (Hokkaido)

Sapporo: *Mitraspora cyprini* Fujita

*Chloromyxum koi* Fujita

*Sphaerospora angulata* Fujita

*Lentospora acuta* (Fujita) Kudo



## 2) Central part (Hondo)

Tokio: *Mitraspora cyprini* Fujita  
*Chloromyxum misgurni* Kudo  
*Chloromyxum fujitai* Kudo  
*Sphaerospora carassii* nov. spec.  
*Myxidium kagayamai* nov. spec.  
*Zschokkella acheilognathi* Kudo  
*Myxosoma dujardini* (?) Thélohan  
*Myxobolus toyamai* Kudo  
*Myxobolus misgurni*, nov. spec.  
*Myxobolus koi* nov. spec.

Numazu: *Myxidium anguillae* Ishii  
*Lentospora dermatobia* Ishii

## 3) Southern part (Kiushiu)

Fukuoka: *Myxobolus* sp. Miyairi  
*Myxobolus miyairii* nov. spec.  
*Henneguya miyairii* nov. spec.

## II INDIA

## A. Myxosporidia of fresh-water fish

Katwan, Mirzapore (U.P.): *Myxobolus* sp. Southwell  
 Mirpur, Decca district: *Myxobolus rohita* Southwell et Prashad  
*Myxobolus seni* Southwell et Prashad  
*Myxobolus nodularis* Southwell et Prashad

## B. Myxosporidian of reptiles

Bombay: *Myxidium mackiei* Bosanquet

## III BURMA

In the vicinity of Ruby Mines: *Sphaerospora* sp. Southwell et Prashad

## IV KAMTSCHATKA

?*Henneguya salminicola* Ward

## AUSTRALIA

## Myxosporidian of amphibia

In the vicinity of Sidney: *Myxobolus hylae* Johnston et Bancroft

## AFRICA

## A. Myxosporidia of fresh-water fish

Nile: *Myxobolus unicapsulatus* Gurley  
*Henneguya strongylura* Gurley

## B. Myxosporidia of marine fish

## 1) Indian Ocean

Algoa Bay: *Chloromyxum magnum* Awerinzew  
 Beira: *Chloromyxum quadratum* Thélohan  
 East London: *Chloromyxum magnum* Awerinzew  
 Lorenzo Marques: *Ceratomyxa tylosuri* Awerinzew  
*Ceratomyxa spari* Awerinzew  
*Ceratomyxa* sp(?). Awerinzew  
*Ceratomyxa* sp (?). Awerinzew  
*Sphaeromyxa exneri* Awerinzew

## 2) South Atlantic Ocean

Lüderitz Bay: *Chloromyxum magnum* Awerinzew

## NORTH AMERICA

## I UNITED STATES

## A. Myxosporidia of fresh-water fish

- 1) From Rivers emptying into Atlantic Ocean
  - Carlisle, Va. (trib. of Potomac River): *Myxobolus transovalis* Gurley
  - Columbia, S. C. (Santee River): *Myxobolus globosus* Gurley
  - Kinston, N. C. (Neuse River): *Myxobolus globosus* Gurley
  - West Falmouth, Mass.: *Myxobolus* sp. Kudo
  - Woodbury, N. J. (Delaware River): *Henneguya monura* Gurley
- 2) From Lakes and Rivers opening into the Gulf of Mexico
  - Fox River, trib. Mississippi: *Myxobolus globosus* Gurley
  - Lake Mendota, Wis.: *Myxidium lieberkühni* Bütschli  
*Henneguya wisconsinensis* Mavor et Strasser
  - Neches River, Palestin, Tex.: *Henneguya macrura* (Gurley) Thélohan
  - Storm Lake, Ia.: *Henneguya gurleyi* Kudo
  - Stony Creek, Ill.: *Chloromyxum trijugum* nov. spec.  
*Myxobolus orbiculatus* nov. spec.  
*Henneguya mictospora* nov. spec.
  - Homer Park, Ill.: *Chloromyxum trijugum* nov. spec.  
*Myxobolus orbiculatus* nov. spec.
  - Salt Fork, Urbana, Ill.: *Wardia ovinocua* nov. gen. nov. spec.  
*Chloromyxum calostomi* nov. spec.  
*Myxobolus discrepans*, nov. spec.
  - Crystal Lake, Urbana, Ill.: *Mitraspora elongata* nov. spec.  
*Myxidium americanum* nov. spec.  
*Myxobolus mesentericus* nov. spec.
- 3) From the rivers opening into the Great Lakes
  - Black River, Ohio: Gen. et spec. incert. Linton
  - Put-In-Bay, Ohio: *Myxobolus aureatus* Ward  
*Henneguya brachyura* Ward

## B. Myxosporidia of marine fish (Atlantic Ocean)

- Beaufort, N. C.:
- Leptotheca fusiformis* Davis
  - Leptotheca scissura* Davis
  - Leptotheca lobosa* Davis
  - Leptotheca glomerata* Davis
  - Ceratomyxa mesospora* Davis
  - Ceratomyxa sphairophora* Davis
  - Ceratomyxa taenia* Davis
  - Ceratomyxa attenuata* Davis
  - Ceratomyxa recurvata* Davis
  - Ceratomyxa lunata* Davis
  - Ceratomyxa abbreviata* Davis
  - Ceratomyxa flagellifera* Davis
  - Ceratomyxa agglomerata* Davis
  - Ceratomyxa amorphia* Davis
  - Ceratomyxa monospora* Davis
  - Ceratomyxa streptospora* Davis
  - Ceratomyxa aggregata* Davis
  - Ceratomyxa undulata* Davis

- Ceratomyxa navicularia* Davis  
*Ceratomyxa spinosa* Davis  
*Myxoproteus cordiformis* Davis  
*Myxoproteus cornutus* Davis  
*Chloromyxum leydi* Mingazzini  
*Chloromyxum granulosum* Davis  
*Sphaerospora polymorpha* Davis  
*Sinuolinea dimorpha* Davis  
*Sinuolinea capsularis* Davis  
*Sinuolinea arborescens* Davis  
*Sinuolinea opacita* Davis  
*Sinuolinea brachiophora* Davis  
*Myxidium incurvatum* Thélohan  
*Myxidium glutinosum* Davis  
*Myxidium phyllium* Davis  
*Sphaeromyxa balbianii* Thélohan  
*Zschokkella globulosa* Davis  
*Myxobolus capsulatus* Davis  
 Woods Hole, Mass.: *Ceratomyxa drepanopsettae* Awerinzew  
*Chloromyxum funduli* Hahn  
*Chloromyxum clupeidae* Hahn  
*Myxosoma funduli* Kudo  
*Myxobolus lintoni* Gurley  
*Myxobolus funduli* Kudo  
*Myxobolus pleuronectidae* Hahn  
 Locality unrecorded: *Henneguya schizura* (Gurley) Labbé  
                                   C. Myxosporidian of Amphibia  
 Sycamore, Ill.: *Wardia ohlmacheri* (Gurley) Kudo

## II CANADA

- A. Myxosporidia of fresh-water fish  
 Georgian Bay (south. part): *Myxidium lieberkuhni* Bütschli  
                                   *Myxobolus notatus* Mavor  
                                   Gen. et spec. incert. Mavor  
 B. Myxosporidia of marine fish (Atlantic Ocean)  
 Passamaquoddy Bay (at or  
   near the mouth of St. Croix  
   River), New Brunswick: *Ceratomyxa acadiensis* Mavor  
                                   *Myxidium bergense* Auerbach  
                                   *M. sp.* Mavor  
                                   Gen. et spec. incert. Mavor

## III ALASKA

- Klutina Lake: *Chloromyxum wardi* nov. spec.  
 Stickeen River: *Henneguya salminicola* Ward

## SOUTH AMERICA

- A. Myxosporidia of fresh-water fish from the waters connected with Atlantic Ocean  
 Guiana: *Myxobolus inaequalis* Gurley  
 Surinam: *Myxobolus inaequalis* Gurley  
 Locality?: *Henneguya linearis* (Gurley) Labbé

## B. Myxosporidian of marine fish (Atlantic Ocean)

Rio de Janeiro: *Myxidium striatum* Cunha et Fonseca

## C. Myxosporidian of Amphibia

Brazil: *Sphaeromyxa immersa* (Lutz) Thélohan

## EUROPE

## I ITALY

## A. Myxosporidia of fresh-water fish from lakes and rivers opening into Adriatic Sea

Lago di Como: *Mitraspora caudata* (Parisi) Kudo*Myxidium lieberkühni* BütschliLago di Garda: *Sphaerospora elegans* Thélohan*Henneguya gasterostei* ParisiLago di Varamo: *Henneguya minula* (Cohn)Lago Maggiore: *Myxidium lieberkühni* BütschliMilano: *Myxidium lieberkühni* Bütschli*Myxobolus pfeifferi* ThélohanPavia: *Myxobolus gigas* Auerbach*Myxobolus ellipsoides* Thélohan*Henneguya peri-intestinalis* CépèdeTicino River: *Henneguya minula* (Cohn)

## B. Myxosporidia of marine fish

## 1) Ligurian Sea

Genova: *Chloromyxum leydigi* MingazziniGen. incert. *merlucii* PerugiaGen. incert. *congrui* Perugia

## 2) Tyrrhenian Sea

Napoli: *Leptotheca agilis* Thélohan*Leptotheca elongata* Thélohan*Ceratomyxa arcuata* Thélohan*Ceratomyxa appendiculata* Thélohan*Ceratomyxa truncata* Thélohan*Ceratomyxa inaequalis* Doflein*Ceratomyxa linotheca* Doflein*Myxoproteus ambiguus* (Thél.) Doflein*Chloromyxum leydigi* Mingazzini*Chloromyxum quadratum* Thélohan*Sphaerospora divergens* Thélohan*Myxidium incurvatum* Thélohan*Myxidium giganteum* Doflein*Myxidium depressum* Parisi*Myxidium oviforme* Parisi*Sphaeromyxa balbianii* Thélohan*Sphaeromyxa incurvata* Doflein*Sphaeromyxa sabraesi* Laveran et Mesnil*Lentospora asymmetrica* Parisi*Myxobolus exiguus* Thélohan*Myxobolus mülleri* Bütschli*Henneguya neapolitana* Parisi

## II MONACO

## Myxosporidia of fish from Ligurian Sea

*Leptotheca elongata* Thélohan*Ceratomyxa sphaerulosa* Thélohan

*Ceratomyxa arcuata* Thélohan  
*Ceratomyxa pallida* Thélohan  
*Ceratomyxa herowardi* Georgévitch  
*Ceratomyxa* sp. Georgévitch  
*Chloromyxum leydigi* Mingazzini  
*Myxidium incurvatum* Thélohan  
*Sphaeromyxa sabrazesi* Laveran et Mesnil

### III FRANCE

#### A. Myxosporidia of fresh-water fish

##### 1) From Rivers opening into Atlantic Ocean

Aigne: *Myxobolus pfeifferi* Thélohan  
 Bretagne: *Sphaerospora elegans* Thélohan  
 Lorraine: *Myxobolus oviformis* Thélohan  
 Nancy: *Myxobolus pfeifferi* Thélohan  
 Marne: *Myxobolus pfeifferi* Thélohan  
 Seine: *Myxobolus pfeifferi* Thélohan  
 Paris: *Chloromyxum fluviatile* Thélohan  
 Wimereux: *Myxidium giardi* Cépède

##### 2) From Rivers opening into Mediterranean Sea

Dauphiné: *Myxobolus mulleri* Bütschli  
 Drac River: *Myxobolus mulleri* Bütschli  
               *Myxobolus pfeifferi* Thélohan  
 Grenoble: *Chloromyxum cristatum* Léger  
 Isère River: *Myxidium barbatulae* Cépède  
               *Myxobolus oviformis* Thélohan  
               *Myxobolus mulleri* Bütschli  
               *Myxobolus cycloides* Gurley  
               *Henneguya légeri* Cépède  
 Lac d'Annecy: *Myxobolus mulleri* Bütschli  
 Lac de Paladru: *Myxobolus cycloides* Gurley  
 Lac du Bourget: *Myxobolus obesus* Gurley  
               *Henneguya peri intestinalis* Cépède  
 Lyon?: *Henneguya tenuis* Vaney et Conte  
 Rhône River: *Myxobolus pfeifferi* Thélohan  
 Saône River: *Myxobolus pfeifferi* Thélohan

#### B. Myxosporidia of marine fish

##### 1) From Atlantic Ocean

Arcachon *Sphaeromyxa sabrazesi* Laveran et Mesnil  
 Concarneau: *Ceratomyxa arcuata* Thélohan  
               *Chloromyxum leydigi* Mingazzini  
               *Chloromyxum quadratum* Thélohan  
               *Sphaerospora divergens* Thélohan  
               *Myxidium incurvatum* Thélohan  
               *Sphaeromyxa balbianii* Thélohan  
 Le Croisic: *Leptotheca elongata* Thélohan  
               *Leptotheca parva* Thélohan  
               *Leptotheca renicola* Thélohan  
               *Ceratomyxa appendiculata* Thélohan  
               *Myxoproteus ambiguus* (Thél.) Doflein  
               *Sphaerospora rostrata* Thélohan

- Concarneau:** *Ceratomyxa arcuata* Thélohan  
*Chloromyxum leydigi* Mingazzini  
*Chloromyxum quadratum* Thélohan  
*Sphaerospora divergens* Thélohan  
*Myxidium incurvatum* Thélohan  
*Sphaeromyxa balbianii* Thélohan
- Roscoff:** *Ceratomyxa sphaerulosa* Thélohan  
*Ceratomyxa arcuata* Thélohan  
*Ceratomyxa appendiculata* Thélohan  
*Chloromyxum leydigi* Mingazzini  
*Chloromyxum quadratum* Thélohan  
*Sphaerospora rostrata* Thélohan  
*Sphaerospora divergens* Thélohan  
*Myxidium incurvatum* Thélohan  
*Myxidium gadi* Georgévitch  
*Sphaeromyxa balbianii* Thélohan  
*Sphaeromyxa sabraesi* Laveran et Mesnil  
*Sphaeromyxa gasterostei* Georgévitch  
*Myxobolus mülleri* Bütschli
- Le-Vivier-sur-mer:** *Leptotheca parva* Thélohan  
*Myxidium sphaericum* Thélohan  
*Myxobolus exiguus* Thélohan
- St.-Valery-en-caux:** *Ceratomyxa sphaerulosa* Thélohan

## 2) From Mediterranean coast

- Marseille:** *Leptotheca elongata* Thélohan  
*Leptotheca parva* Thélohan  
*Leptotheca renicola* Thélohan  
*Leptotheca hepseti* Thélohan  
*Ceratomyxa arcuata* Thélohan  
*Ceratomyxa pallida* Thélohan  
*Ceratomyxa globulifera* Thélohan  
*Ceratomyxa appendiculata* Thélohan  
*Ceratomyxa reticularis* Thélohan  
*Chloromyxum leydigi* Mingazzini  
*Sphaerospora rostrata* Thélohan  
*Myxidium incurvatum* Thélohan  
*Myxidium sphaericum* Thélohan  
*Sphaeromyxa balbianii* Thélohan  
*Myxobolus exiguus* Thélohan
- Banyuls:** *Leptotheca elongata* Thélohan  
*Leptotheca polymorpha* (Thél.) Labbé  
*Ceratomyxa arcuata* Thélohan  
*Ceratomyxa globulifera* Thélohan  
*Ceratomyxa appendiculata* Thélohan  
*Ceratomyxa reticularis* Thélohan  
*Chloromyxum leydigi* Mingazzini  
*Sphaerospora rostrata* Thélohan  
*Myxidium incurvatum* Thélohan  
*Myxidium sphaericum* Thélohan  
*Sphaeromyxa balbianii* Thélohan  
*Myxobolus exiguus* Thélohan

- Villefranche: *Ceratomyxa pallida* Thélohan  
*Ceratomyxa truncata* Thélohan  
*Ceratomyxa coris* Georgévitch  
*Sphaeromyxa balbianii* Thélohan
- Locality unknown: *Leptotheca agilis* Thélohan  
*Leptotheca perlata* (Gurley) Labbé  
*Myxidium lieberkühni* Bütschli  
*Myxidium histophilum* Thélohan  
*Myxosoma dujardini* Thélohan  
*Myxobolus piriformis* Thélohan  
*Myxobolus dispar* Thélohan  
*Myxobolus obesus* Thélohan  
*Henneguya psorospermica* Thélohan  
*Henneguya media* Thélohan  
*Henneguya brevis* Thélohan  
*Hoferellus cyprini* Doflein  
C. Myxosporidian in a reptile  
*Myxidium danilewskyi* Laveran

## IV GERMANY

## A. Myxosporidia of fresh-water fish

## 1) From Rivers opening into North Sea

- Throughout country: *Myxobolus cyprini* Doflein
- Berlin: *Henneguya oviperda* (Cohn)
- Bodensee: *Chloromyxum dubium* Auerbach  
*Myxobolus mülleri* Bütschli
- Gutach: *Myxobolus neurobius* Schubert et Schröder  
*Henneguya nüsslii* Schub. et Schröder
- Karlsruhe and its vicinity: *Chloromyxum mucronatum* Gurley  
*Sphaerospora elegans* Thélohan  
*Myxidium lieberkühni* Bütschli  
*Myxidium pfeifferi* Auerbach  
*Myxidium macrocapsulare* Auerbach  
*Henneguya oviperda* (Cohn)  
*Henneguya lobosa* (Cohn)  
*Myxobolus gigas* Auerbach
- Leipzig: *Myxobolus* sp. Gurley
- Mosel: *Myxobolus pfeifferi* Thélohan  
*Myxobolus squamae* Keysselitz  
*Myxobolus cordis* Keysselitz  
*Myxobolus musculi* Keysselitz
- Neckar: *Myxobolus exiguus* Thélohan (Heidelberg)  
*Myxobolus mülleri* Bütschli  
*Myxobolus pfeifferi* Thélohan  
*Myxobolus squamae* Keysselitz  
*Myxobolus cordis* Keysselitz  
*Myxobolus musculi* Keysselitz  
*Henneguya psorospermica* Thélohan  
*Henneguya acerinae* Schröder (Heidelberg)
- Rhine: *Myxidium lieberkühni* Bütschli  
*Myxobolus mülleri* Bütschli  
*Henneguya psorospermica* Thélohan  
*Lentospora encephalina* Mulsow

## 2) From Rivers opening into Baltic Sea

- Alle:** *Myxobolus mülleri* Bütschli  
**Frisches Haff:** *Myxidium lieberkühni* Bütschli  
*Myxosoma dujardini* Thélohan  
*Myxobolus piriformis* Thélohan  
*Myxobolus dispar* Thélohan  
*Myxobolus exiguus* Thélohan  
*Myxobolus oviformis* Thélohan  
*Myxobolus mülleri* Bütschli  
*Myxobolus cycloides* Gurley  
*Myxobolus anurus* Cohn  
*Myxobolus* sp. Wegener  
*Myxobolus permagnus* Wegener  
*Henneguya psorospermica* Thélohan  
*Henneguya texta* (Cohn)  
*Henneguya minula* (Cohn)  
*Henneguya lobosa* (Cohn)  
*Henneguya creplini* (Gurley)  
**Kurisches Haff:** *Myxosoma dujardini* Thélohan  
*Myxobolus exiguus* Thélohan  
*Myxobolus oviformis* Thélohan  
*Myxobolus cycloides* Gurley  
*Henneguya psorospermica* Thélohan  
*Henneguya texta* (Cohn)  
*Henneguya creplini* (Gurley) Labbé  
**Masurische Seen:** *Sphaerospora masovica* Cohn  
*Myxobolus dispar* Thélohan  
*Myxobolus ellipsoides* Thélohan  
*Myxobolus cycloides* Gurley  
*Myxobolus anurus* Cohn  
*Henneguya psorospermica* Thélohan  
*Henneguya texta* (Cohn)  
**Pregel:** *Myxosoma dujardini* Thélohan  
*Myxobolus piriformis* Thélohan  
*Myxobolus dispar* Thélohan  
*Myxobolus exiguus* Thélohan  
*Myxobolus oviformis* Thélohan  
*Myxobolus mülleri* Bütschli  
*Myxobolus cycloides* Gurley  
*Myxobolus anurus* Cohn  
*Myxobolus permagnus* Wegener  
*Henneguya psorospermica* Thélohan  
*Henneguya texta* (Cohn)  
*Henneguya minula* (Cohn)  
*Henneguya lobosa* (Cohn)  
*Henneguya creplini* (Gurley) Labbé  
**Weichsel:** *Myxobolus cyprini* Doflein

- 3) Localities unknown:** *Chloromyxum leydi* Mingazzini  
*Myxidium lieberkühni* Bütschli  
*Myxidium* sp. Gurley  
*Lentospora cerebrealis* (Hofer) Plehn



*Henneguya schisura* (Gurley) Labbé  
*Hoyerellus cyprini* Doflein  
 Gen. et spec. incert. Leydig  
 Gen. et spec. incert. Leydig  
 Gen. et spec. incert. Leydig  
 Gen. et spec. incert. Borne

## V NETHERLAND

Myxosporidian of marine fish  
 Helder: *Chloromyxum quadratum* Thélohan

## VI ENGLAND

Myxosporidia of marine fish  
 Firth of Clyde, More-  
 camb, etc.: *Myxobolus aeglefini* Auerbach  
 Liverpool (?): *Sphaerospora platessae* Woodcock

## VII NORWAY

Myxosporidia of marine fish  
 Abelvaer: *Myxidium bergense* Auerbach  
*Myxidium oviforme* Parisi  
*Zschokkella hildae* Auerbach  
*Myxobolus aeglefini* Auerbach  
 Bergen: *Leptotheca parva* Thélohan  
*Leptotheca macrospora* Auerbach  
*Leptotheca informis* Auerbach  
*Leptotheca longipes* Auerbach  
*Ceratomyxa sphaerulosa* Thélohan  
*Myxidium incurvatum* Thélohan  
*Myxidium inflatum* Auerbach  
*Myxidium bergense* Auerbach  
*Myxidium procerum* Auerbach  
*Sphaeromyxa hellandi* Auerbach  
*Zschokkella hildae* Auerbach  
*Myxobolus aeglefini* Auerbach  
 Bergsfjord: *Myxidium bergense* Auerbach  
*Zschokkella hildae* Auerbach  
 Boadsfjord: *Zschokkella hildae* Auerbach  
 Bodø: *Myxidium bergense* Auerbach  
*Zschokkella hildae* Auerbach  
 Finkongkjeilen: *Myxidium bergense* Auerbach  
*Zschokkella hildae* Auerbach  
 Grønøy: *Myxidium bergense* Auerbach  
*Zschokkella hildae* Auerbach  
 Hammerfest: *Myxidium bergense* Auerbach  
*Myxidium oviforme* Parisi  
*Zschokkella hildae* Auerbach  
 Harstad: *Myxidium bergense* Auerbach  
*Zschokkella hildae* Auerbach  
 Honnigsvaag: *Myxidium bergense* Auerbach  
*Zschokkella hildae* Auerbach  
 Kabelvaag: *Ceratomyxa drepanopsettae* Awerinzew

	<i>Myxidium bergense</i> Auerbach
	<i>Zschokkella hildae</i> Auerbach
Kilberg:	<i>Zschokkella hildae</i> Auerbach
Kirkenes:	<i>Myxidium bergense</i> Auerbach
Kristiana:	<i>Myxidium bergense</i> Auerbach
Kristiansand:	<i>Leptotheca parva</i> Thélohan
	<i>Leptotheca macrospora</i> Auerbach
	<i>Myxidium oviforme</i> Parisi
	<i>Zschokkella hildae</i> Auerbach
Lödingen:	<i>Myxobolus aeglefini</i> Auerbach
Makur:	<i>Myxidium bergense</i> Auerbach
	<i>Zschokkella hildae</i> Auerbach
Mosjøen:	<i>Zschokkella hildae</i> Auerbach
	<i>Myxidium bergense</i> Auerbach
Nusfjord:	<i>Myxidium bergense</i> Auerbach
	<i>Zschokkella hildae</i> Auerbach
Rörvik:	<i>Ceratomyxa drepanopsettae</i> Awerinzew
	<i>Myxidium bergense</i> Auerbach
Rossfjord:	<i>Myxidium oviforme</i> Parisi
Skjervø:	<i>Zschokkella hildae</i> Auerbach
Skjöttningsberg:	<i>Zschokkella hildae</i> Auerbach
	<i>Myxidium bergense</i> Auerbach
Smalfjorden:	<i>Sphaerospora divergens</i> Thélohan
	<i>Zschokkella hildae</i> Auerbach
Stavanger:	<i>Leptotheca parva</i> Thélohan
	<i>Myxidium bergense</i> Auerbach
Svolvaer:	<i>Myxidium bergense</i> Auerbach
	<i>Zschokkella hildae</i> Auerbach
Tjømø:	<i>Leptotheca informis</i> Thélohan
	<i>Ceratomyxa drepanopsettae</i> Awerinzew
	<i>Myxidium bergense</i> Auerbach
Torghatten:	<i>Sphaeromyxa hellandi</i> Auerbach
Trondhjem:	<i>Myxidium bergense</i> Auerbach
	<i>Myxidium oviforme</i> Parisi
	<i>Zschokkella hildae</i> Auerbach
Vikholmen:	<i>Zschokkella hildae</i> Auerbach
Vardø:	<i>Myxidium bergense</i> Auerbach
	<i>Myxidium oviforme</i> Parisi
	<i>Zschokkella hildae</i> Auerbach
	<i>Myxobolus aeglefini</i> Auerbach

## VIII SWITZERLAND

## Myxosporidia of fresh-water fish

- 1) From Lakes connected with North Sea
 

Neuchatel:	<i>Myxobolus fuhrmanni</i> Auerbach
	<i>Myxobolus mülleri</i> Bütschli
	<i>Henneguya oviperda</i> (Cohn)
	<i>Henneguya zschokkei</i> (Gurley) Doflein
Thun:	<i>Henneguya zschokkei</i> (Gurley) Doflein
Zurich:	<i>Henneguya zschokkei</i> (Gurley) Doflein
Lucerne:	<i>Myxosoma dujardini</i> Thélohan
	<i>Myxobolus ellipsoides</i> Thélohan

- Myxobolus oviformis* Thélohan  
*Myxobolus mülleri* Bütschli  
*Henneguya psorospermica* Thélohan  
*Henneguya texta* (Cohn)  
*Henneguya zschokkei* (Gurley) Doflein  
 Gen. et spec. incert. Nufer  
 Wallen: *Henneguya zschokkei* (Gurley) Doflein  
 2) From Lake connected with Mediterranean Sea  
 Geneva: *Myxobolus sphaeralis* Gurley  
*Henneguya zschokkei* (Gurley) Doflein

## IX AUSTRIA

## A. Myxosporidia of fresh-water fish

- 1) From Rivers opening into Black Sea  
 Danube tributaries and Neusiedler: *Chloromyxum thymalli* Lebzelter  
*Myxosoma* (?) *lobatum* Nemeček  
*Myxobolus aeglefini* Auerbach  
*Myxobolus cyprini* Doflein  
*Myxobolus rotundus* Nemeček  
*Myxobolus minutus* Nemeček  
*Myxobolus* sp. Lebzelter  
*Henneguya acerinae* Schröder  
*Henneguya gigantea* Nemeček  
 2) From Rivers opening into North Sea  
 Prag: *Myxosoma dujardini* Thélohan  
*Myxobolus ellipsoides* Thélohan  
*Myxobolus oculi-leucisci* Trojan  
 Krakau: *Myxobolus cyprini* Doflein  
 B. Myxosporidia of marine fish (Adriatic Sea)  
 Rovigno: *Leptotheca agilis* Thélohan  
*Ceratomyxa pallida* Thélohan  
*Ceratomyxa appendiculata* Thélohan  
*Myxoproteus ambiguus* (Thél.) Doflein  
*Chloromyxum leydi* Mingazzini  
*Sphaeromyxa sabraesi* Laveran et Mesnil  
 Locality unknown: Gen. et spec. incert. Heckel et Kner

## C. Myxosporidian of Amphibia

- Vienna: *Chloromyxum protei* Joseph

## X SERBIA

- Pergrad (Danube): *Henneguya gigantea* Nemeček

## XI RUSSIA

## A. Myxosporidia of fresh-water fish

- Volga (to Caspian Sea): *Lentospora multiplicata* Reuss  
*Myxobolus volgensis* Reuss  
*Myxobolus scardinii* Reuss  
*Myxobolus physophilus* Reuss  
*Myxobolus macrocapsularis* Reuss  
*Myxobolus sandrae* Reuss  
*Myxobolus bramae* Reuss  
*Myxobolus cyprinicola* Reuss  
*Myxobolus balleri* Reuss

- Don (to Black Sea): *Myxobolus* sp. Gurley  
 Locality unknown: *Zschokkella nova* Klokacewa  
*Myxobolus magnus* Awerinzew  
*Myxobolus carassii* Klokacewa  
*Henneguya kolesnikovii* (Gurley) Labbé

B. Myxosporidia of marine fish from Arctic Ocean

- Murman coast: *Ceratomyxa ramosa* Awerinzew  
*Ceratomyxa drepanopsellae* Awerinzew  
*Myxidium* sp. Awerinzew  
*Leptotheca* sp. Awerinzew  
*Chloromyxum* sp. Awerinzew

B. DISTRIBUTION OF MYXOSPORIDIA IN ANIMALS

The number of host species that harbor Myxosporidia is 237, as will be seen from List III.

The two incompletely studied forms are found in Annelida and Insecta, Myxosporidia are the parasites of Vertebrata, especially of Pisces, only few being found infecting Amphibia and Reptilia. They are distributed among these groups of animals as follows:

	Number of host species
Annelida	1
Insecta	1
Pisces	223
Amphibia	8
Reptilia	4

Gurley (1894:101-105), Wasielewsky (1896:132-148), Labbé (1899:133-161) and Auerbach (1910:36-45; 1911:471-494) gave lists in which they recorded the names of host species. Wasielewsky arranged the names alphabetically while others listed them according to their systematic order. In the following pages, the writer followed Wasielewsky, i.e., the names of the host species are arranged alphabetically as is supposed to be more convenient in referring to the host than any form presented otherwise.

LIST III. LIST OF HOST SPECIES

Host	Organ Infected	Myxosporidian	Locality
Annelida			
<i>Nais lacustris</i> (N. proboscidea)	Unknown	<i>Myxobolus</i> sp.	Germany
Insecta			
<i>Tortrix viridana</i> L. (imago)	Abdominal cavity	<i>Chloromyxum diploxyis</i>	France
Pisces			
<i>Abramis ballerus</i> L.	Branchiae	<i>Myxobolus balleri</i>	Russia
<i>A. brama</i> L.	"	<i>bramae</i>	"

Host	Organ Infected	Myxosporidian	Locality
	Branchiae	<i>Myxobolus cycloides</i>	Germany
	"	<i>ellipsoides</i>	" (?)
	"	<i>exiguus</i>	France
	"	<i>oviformis</i>	France
	"	<i>rotundus</i>	Austria
	Gall-bladder	<i>Sphaerospora masonica</i>	Germany
	Kidney	<i>Myxobolus cyprini</i>	" , Hungary
	Subcut. conn. tissue of oper- culum	<i>gigas</i>	Germany, Italy
<i>A. vimba</i> L.....	Branchiae	<i>cycloides</i>	Germany
	"	<i>ellipsoides</i>	" (?)
	"	<i>oviformis</i>	Germany
<i>Acanthias acanthias</i> L.....	Gall-bladder	<i>Chloromyxum leydigi</i>	France
<i>A. blainvillei</i> .....	"	<i>magnum</i>	Africa
<i>Acerina cernua</i> L.....	Branchiae	<i>Henneguya acerinae</i>	Germany
	" , Muscle	<i>creplini</i>	"
	Conn. tissue of aliment. canal	<i>tenuis</i>	France
	Eye	<i>Myxobolus magnus</i>	Russia
	Muscle	<i>Leptotheca perlata</i>	France?
<i>Acheilognathus lanceolatum</i> Temm. et Schl.....	Gall-bladder, Gall-duct	<i>Zschokkella acheilognathi</i>	Nippon
<i>Alburnus alburnus</i> L.....	Branchiae	<i>Myxobolus cycloides</i>	Germany
( <i>A. lucidus</i> Heck)	"	<i>dispar</i>	"
	"	<i>ellipsoides</i>	Germany ?
	"	<i>oviformis</i>	France
	" , kidney	<i>obesus</i>	"
	Muscle and spleen	<i>dispar</i>	"
	Eye	<i>mülleri</i>	Switzerland
<i>Alosa finta</i> Cuv. var. <i>lacus-</i> <i>tris</i> Fatio.....	Kidney	<i>Mitraspora caudata</i>	Italy
<i>Ameiurus melas</i> Raf.....	Base of spines of 2nd dorsal fin	<i>Henneguya gurleyi</i>	U. S. A.
<i>Ancylopussetta quadrocellata</i> Gill.....	Gall-bladder	<i>Ceratomyxa undulata</i>	"
<i>Anguilla japonica</i> Temm. et Schl.....	Integument "	<i>Myxidium anguillae</i> <i>Lentospora dermatobia</i>	Nippon "
<i>A. vulgaris</i> Flemm.....	Kidney	<i>Myxidium giardi</i>	France
<i>Aphredoderus sayanus</i> Gill.	Subcutaneous intermusc. tiss.	<i>Henneguya monura</i>	U. S. A.
<i>Apogon rex-mullorum</i> Cuv.	Gall-bladder	<i>Myxidium oviforme</i>	Italy
<i>Argentina silus</i> Nilss.....	"	<i>procerum</i>	Norway
<i>Argodes polystaphylodon</i> .....	Muscle	<i>Chloromyxum quadratum</i>	Africa
<i>Aspius rapax</i> Ag.....	Branchiae	<i>Myxosoma(?) lobatum</i>	Austria
<i>Aspro asper</i> L.....	"	<i>Myxobolus mülleri</i>	France
<i>A. singei</i> Cuv.....	"	<i>Henneguya acerinae</i>	"

Host	Organ Infected	Myxosporidian	Locality
<i>Atherina hepsetus</i> L.....	Gall-bladder	<i>Leptotheca hepseti</i>	France
<i>Bairdiella chrysura</i> .....	Urin. bladder	<i>Myxoproteus cornutus</i>	U. S. A.
<i>B. rouckus</i> Cuv. et Val.....	Gall-bladder	<i>Myxidium striatum</i>	Brazil
<i>Barbus barbatus</i> L..... ( <i>B. fluviatilis</i> )	Kidney, spleen, intestine, ovary, etc.	<i>Myxobolus pfeifferi</i>	France, Germany
	Inner surface of scale	<i>squamae</i>	Germany
	Muscle of ven- tricle	<i>cordis</i>	"
	Muscle, kidney	<i>musculi</i>	"
<i>B. plebejus</i> Val .... .	"	<i>pfeifferi</i>	Italy
<i>B. vulgaris</i> Flem..... .	Branchiae	<i>mülleri</i>	Germany
<i>Barilius barna</i> ..... .	Under scales	<i>Sphaerospora</i> sp.	Burma
<i>Belone acus</i> Risso .... .	Gall-bladder	<i>Myxidium sphaericum</i>	France
<i>B. belone</i> L. . . . .	"	<i>Myxidium sphaericum</i>	"
<i>Blennius ocellatus</i> . . . . .	"	<i>Sphaeromyxa incurvata</i>	Italy
<i>B. gattorugine</i> Brunn .	Kidney	<i>Chloromyxum quadratum</i>	"
<i>B. pholis</i> L .....	Gall-bladder	<i>Myxidium incurvatum</i>	France
	Renal tubules	<i>Sphaerospora divergens</i>	"
<i>Blicca björkna</i> L	Branchiae	<i>Myxobolus cycloides</i>	Germany
	"	<i>ellipsoides</i>	" ?
	"	<i>macrocapsularis</i>	Russia
	"	<i>oviformis</i>	Germany
<i>Box boops</i> L ..	Gall-bladder	<i>Ceratomyxa pallida</i>	France, Italy
<i>B. salpa</i> L ...	Gall-bladder	<i>Ceratomyxa herouardi</i>	Monaco
	"	<i>pallida</i>	France, Italy
	Kidney	<i>Henneguya neapolitana</i>	Italy
<i>Brevoortia tyrannus</i> Latr	Muscle	<i>Chloromyxum clupeidae</i>	U. S. A.
<i>Brosimius brosmie</i> Ascanius	Gall-bladder	<i>Leptotheca longipes</i>	Norway
	"	<i>Sphaeromyxa hellandi</i>	"
<i>Callionymus lyra</i> L	"	<i>Myxidium incurvatum</i>	France, Norway
	Muscle	<i>Chloromyxum quadratum</i>	France
<i>Carassius auratus</i> L	Branchiae	<i>Lentospora acuta</i>	Nippon
	Kidney	<i>Sphaerospora angulata</i>	"
	"	<i>Mitraspora cyprini</i>	"
	Subcutaneous tiss. of head	<i>Henneguya myairii</i>	"
( <i>C. carassius</i> L.) . .	Body cavity	<i>Myxobolus</i> sp.	Germany
	Branchiae	<i>dispar</i>	"
	"	<i>Sphaerospora carassii</i>	Nippon
( <i>C. vulgaris</i> L.) . . . .	Body cavity, liver, intestine	<i>Myxobolus carassii</i>	Russia
<i>Carcharhinus limbatus</i> .....	Gall-bladder	<i>Zschokkella nova</i>	"
	"	<i>Chloromyxum leydigi</i>	U. S. A.
<i>C. sp</i> .....	"	<i>Ceratomyxa flagellifera</i>	"

Host	Organ Infected	Myxosporidian	Locality
<i>Carpiodes difformis</i> .	Branchiae	<i>Myxobolus discrepans</i>	U S A.
<i>Catostomus commersonii</i> Lac. . . . .	Gall-bladder	<i>Chloromyxum catostomi</i>	"
<i>Centronotus gunellus</i>	"	<i>Sphaeromyxa hellandi</i>	Norway
<i>Cepola rubescens</i> L.	"	<i>balbianii</i>	France
<i>Cestracion tiburo</i> .	"	<i>Chloromyxum leydigi</i>	U. S. A.
<i>C. zygaena</i>	"	<i>Ceratomyxa mesospora</i>	"
	"	<i>Ceratomyxa mesospora</i> <i>recurvata</i>	"
	"	<i>Chloromyxum leydigi</i>	"
<i>Chaetodipterus faber</i>	Gall-bladder	<i>Leptotheca fusiformis</i>	"
	Urin. bladder	<i>Ceratomyxa streptospora</i>	"
<i>Chondrostoma nasus</i> L.	Branchiae	<i>Myxoproteus cordiformis</i>	"
	"	<i>Myxobolus exiguus</i>	Germany
	Tongue	Gen. et spec. incert.	Switzerland
<i>Citharus linguata</i> Gthr	Gall-bladder	Gen et spec. incert.	?
<i>Clupea harengus</i> Young	Gall-bladder	<i>Myxidium depressum</i>	Italy
	"	<i>Ceratomyxa sphaerulosa</i>	Norway
	Muscle	<i>Chloromyxum clupeidae</i>	U. S. A.
<i>C. pilchardus</i> Walb. ( <i>Alosa sardina</i> )	Gall-bladder	<i>Ceratomyxa truncata</i>	France, Italy
	"	<i>Sphaeromyxa balbianii</i>	Italy
<i>Cobitis barbatula</i> L.	Kidney	<i>Myxidium barbatulae</i>	France
	Urin. bladder	<i>Henneguya legeri</i>	"
<i>C. fossilis</i> L.	Branchiae,		
<i>Conger conger</i> L. ( <i>Leptocephalus c.</i> )	kidney, spleen	<i>Myxobolus piriformis</i>	Germany
<i>Coregonus lavaretus</i> L. ( <i>C. fera</i> )	Gall-bladder	Gen incert. <i>congru</i>	Italy
	Branchiae	<i>Henneguya</i> sp.	France?
	" (mucosa)	<i>Myxobolus sphaeralis</i>	Switzerland
	Muscle	<i>Henneguya kolesnikov</i>	Russia
	"	<i>zschokkei</i>	Switzerland
<i>C. exiguus albellus</i>	" , branchia	"	"
<i>C. wartmanni nobilis</i>	" "	"	"
<i>Coris giofredi</i> Risso	Gall-bladder	<i>Ceratomyxa coris</i>	France
<i>C. julis</i> L.	"	"	"
	Muscle	<i>Chloromyxum quadratum</i>	"
	Gall-bladder	<i>Myxidium oviforme</i>	Italy
<i>Cottus gobis</i> L.	Branchiae	<i>Myxobolus mulleri</i>	France
<i>C. scorpius</i> . .	"	<i>Myxidium</i> sp.	Russia
<i>Crenilabrus mediterraneus</i>	"	<i>Ceratomyxa inaequalis</i>	Italy
<i>C. melops</i> L. ....	Eye	<i>Myxobolus mulleri</i>	Germany
			France
	Gall-bladder	<i>Ceratomyxa arcuata</i>	France
	Kidney	<i>Sphaerospora divergens</i>	"
<i>C. pavo</i> Cuv. et Val..	Gall-bladder	<i>Ceratomyxa inaequalis</i>	Italy
	Kidney	<i>Lentospora asymmetrica</i>	Italy
	"	<i>Sphaerospora divergens</i>	France, Italy
<i>Cyclopterus lumpus</i> L.	Gall-bladder	<i>Myxidium inflatum</i>	Norway

Host	Organ Infected	Myxosporidian	Locality
<i>Cynoscion regalis</i>	Gall-bladder	<i>Myxidium glutinosum</i>	U. S. A.
	Urin. bladder, ureters	<i>Sinuolinea dimorpha</i>	"
<i>Cyprinodon variegatus</i>	Subcutaneous tissue	<i>Myxobolus lintoni</i>	"
	Visceral conn. tissue	<i>capsulatus</i>	"
<i>Cyprinus carpio</i> L	Branchiae	<i>cyprinicola</i>	Russia
	"	<i>dispar</i>	France, Germany
	"	<i>oviformis</i>	France ?
	"	<i>toyamae</i>	Nippon
	"	<i>Myxosoma dujardini</i>	France
	"	<i>Myxobolus koi</i>	Nippon
	Brain	<i>Leniospora encephalina</i>	Germany
	Gall-bladder	<i>Chloromyxum koi</i>	Nippon
	Kidney	<i>Hoferellus cyprini</i>	Germany, France
	" liver, spl	<i>Myxobolus cyprini</i>	Germany, Hungary
	Kidney	<i>Mitraspora cyprini</i>	Nippon
	"	<i>Sphaerospora angulata</i>	"
<i>C. (Rasbora) daniconius</i> Day	Subcutaneous intermuscular tissue	<i>Myxobolus</i> sp	India
	Muscles	<i>Myxobolus nodularis</i>	India
<i>Dasybatis hastatus</i>	Gall-bladder	<i>Chloromyxum leydygi</i>	U. S. A.
	"	<i>Leptotheca scissura</i>	"
<i>D. sabina</i>	"	<i>Chloromyxum leydygi</i>	"
<i>Drepanopsetta platessoides</i> Fabr	"	<i>Ceratomyxa drepanopsettae</i>	Russia
<i>Erimyzon sucetta oblongus</i> Lac ( <i>Calostomus tuberculatus</i> )	Branchiae	<i>Myxobolus globosus</i>	U. S. A.
	Integument	<i>oblongus</i>	"
<i>Esox lucius</i> L ..	Branchiae	<i>anurus</i>	Germany
	"	<i>Henneguya lobosa</i>	"
	"	<i>Henneguya psorospermica</i>	France, Germany
	Intestinal wall	<i>Henneguya peri-intestinalis</i>	France, Italy
	Eye muscle, etc.	<i>Henneguya schizura</i>	U. S. A.
	Ovary	<i>Henneguya oviperda</i>	Germany, Switzerland
	Urin. bladder	<i>Myxidium lieberkuhni</i>	France, Italy, Canada, U. S. A., Germany
<i>Fundulus</i> sp	Muscle	<i>Chloromyxum funduli</i>	U. S. A.



Host	Organ Infected	Myxosporidian	Locality
<i>F. diaphanus</i> .....	Muscle	<i>Myxobolus funduli</i>	U. S. A.
<i>F. heteroclitus</i> .....	Branchiae, Muscle	<i>Myxobolus funduli</i>	"
	Branchiae	<i>Myxosoma funduli</i>	"
<i>F. majalis</i> .....	"	<i>Myxosoma funduli</i>	"
	" , muscle	<i>Myxobolus funduli</i>	"
	Gall-bladder	<i>Myxidium incurvatum</i>	"
<i>Gadus aeglefinis</i> L.....	Cartilage	<i>Myxobolus aeglefini</i>	Germany
	Urin. bladder	<i>Zschokkella hildae</i>	Norway
<i>G. callarias</i> L.....	Cartilage	<i>Myxobolus aeglefini</i>	Germany
	Gall-bladder	<i>Myxidium oviforme</i>	Norway
	Urin. bladder	<i>Zschokkella hildae</i>	Norway
<i>G. esmarkii</i> Nilas.....	Cartilage, bone of cranium, eye	<i>Myxobolus aeglefini</i>	Germany, England
<i>G. merlangus</i> L.....	Gall-bladder	<i>Leptotheca informis</i>	Norway
	Cartilage	<i>Myxobolus aeglefini</i>	Germany
<i>G. morrhua</i> L.....	Cartilage	<i>Myxobolus aeglefini</i>	Germany
<i>G. pollackius</i> L.....	Gall-bladder	<i>Myxidium gadi</i>	France
<i>G. virens</i> L.....	"	<i>bergense</i>	Norway
	Urin. bladder	<i>Zschokkella hildae</i>	"
<i>Galeocerca tigrinus</i> .....	Gall-bladder	<i>Ceratomyxa lunata</i>	U. S. A.
<i>Galeus galeus</i> L. ( <i>G. canis</i> )..	"	<i>sphaerulosa</i>	France
<i>Gambusia affinis</i> .....	"	<i>Myxidium incurvatum</i>	U. S. A.
	"	<i>phyllium</i>	"
<i>Gasterosteus aculeatus</i> .....	Kidney (r. t.), ovary	<i>Henneguya media</i>	France
	"	<i>brevis</i>	"
	"	<i>Sphaerospora elegans</i>	" , Italy
	Kidney	<i>Henneguya gasterostei</i>	Italy
<i>G. pungitius</i> L.....	" (r. t.), ovary	<i>brevis</i>	France
	"	<i>media</i>	"
	"	<i>Sphaerospora elegans</i>	"
<i>G. spinachia</i> .....	Gall-bladder	<i>Sphaeromyxa gasterostei</i>	"
<i>Gobio gobio</i> L. ( <i>G. fluviatilis</i> ).....	Fin	<i>Myxobolus mülleri</i>	Germany
	Fin, spleen, kidney, liver	<i>oviformis</i>	France
	Branchiae	<i>cycloides</i>	Germany
<i>Gobius fluviatilis</i> L.....	Body-cavity	Gen. et. spec. incert.	"
<i>Gobius paganellus</i> L.....	Gall-bladder	<i>Ceratomyxa arcuata</i>	Italy
<i>Heliasas chromis</i> Gthr.....	"	<i>Ceratomyxa arcuata</i>	Italy, Monaco
<i>Hippocampus brevisrostris</i> Cuv.....	"	<i>Myxidium incurvatum</i>	Italy
	"	<i>Sphaeromyxa sabrazesi</i>	France, Italy, Hungary

Host	Organ Infected	Myxosporidian	Locality
<i>H. guttulatus</i> Cuv .....	Gall-bladder	<i>Sphaeromyxa sabraresi</i>	Fr., Hun.,
<i>Hippoglossoides liman-</i>	Urin. bladder	<i>Sphaerospora divergens</i>	Monaco
<i>doides</i> .....			Norway
<i>Hippoglossus vulgaris</i>	Gall-bladder	<i>Ceratomyxa drepanopsellae</i> <i>ramosa</i>	Norway
Flemm.....	"		Russia
<i>Hybognathus nuchalis</i> Ag	Conn. tissue of the head	<i>Henneguya macrura</i>	U. S. A.
<i>Idus melanotus</i> Heck ..	Branchiae	<i>Myxobolus ellipsoides</i>	Germany?
	Muscle	<i>Lentospora multiplicata</i>	Russia
<i>Labeo rohita</i> ....	Branchiae	<i>Myxobolus rohita</i>	India
	Fins	<i>Myxobolus seni</i>	"
<i>Labeo niloticus</i> Forsk .	?	<i>Myxobolus unicipsulatus</i>	Egypt
<i>Labrus turdus</i>	Gall-bladder	<i>Ceratomyxa linozpora</i>	Italy
<i>Leiostomus xanthurus</i> .	"	<i>aggregata</i>	U. S. A.
<i>Lepisosteus platystomus</i>	Urinary bladder	<i>Sphaerospora</i> sp.	"
<i>Lepomis cyanellus</i> Raf	Mesentery	<i>Myxobolus mesentericus</i>	"
	Urin. bladder	<i>Henneguya mictospora</i>	"
	Kidney	<i>Mitraspora elongata</i>	"
<i>L. humilis</i> Girard	Ovary	<i>Wardia ovinocua</i>	"
	Urinary bladd.	<i>Henneguya mictospora</i>	"
<i>L. megalotis</i> Raf	Gall-bladder	<i>Chloromyxum trijugum</i>	"
<i>Leuciscus cephalus</i> ( <i>Squalis</i> <i>cephalus</i> ).	Air-bladder, branchiae	<i>Myxobolus mulleri</i> <i>ellipsoides</i>	France,
	Branchiae		Germany
	Gall-bladder	<i>Chloromyxum fluviatile</i>	"
<i>L. lucius</i> L	Branchiae	<i>Myxobolus</i> sp.	France
<i>L. phoxinus</i> L. ( <i>Phoxinus</i> <i>laevis</i> Ag )	Conn tiss of kidney, ovary	<i>Myxidium histophilum</i>	Germany?
	"	<i>Myxobolus mulleri</i>	France
<i>L. rutilus</i> L	Branchiae	<i>ellipsoides</i>	"
	"	<i>mulleri</i>	Germany?
	"	<i>Myxosoma dujardini</i>	"
	Conn tiss. un- der the mouth		France
	muc. mem- brane	<i>Myxobolus fuhrmanni</i>	Switzerland
	Opercle, pseu- do branchiae,		France,
	kidney	<i>cycloides</i>	Germany
	Vitreous body of eye	<i>oculi-leucisci</i>	Austria
	?	<i>Henneguya</i> sp.	Germany
	Heart	Gen. et spec. incert.	"
<i>Leuciscus</i> sp	Branchiae	<i>Myxobolus minutus</i>	Austria
	"	<i>Myxosoma</i> (?) <i>lobatum</i>	"
<i>Iophius budegassa</i> Spin	Gall-bladder	<i>Ceratomyxa appendiculata</i>	Italy,
			France
<i>L. piscatorius</i> L .	"	<i>Ceratomyxa appendiculata</i>	"

Host	Organ Infected	Myxosporidian	Locality
<i>L. piscatorius</i> L	Urin. bladder	<i>Myxoproteus ambiguus</i>	France, Italy, Hungary
<i>Lota lota</i> L. ( <i>L. vulgaris</i> )	Branchiae	<i>Myxobolus mulleri</i>	Germany
	"	<i>Myxobolus cycloides</i>	Germany
	Gall-bladder	<i>Chloromyxum dubium</i>	" , Austria
	Urin. bladder, kidney	<i>mucronatum</i>	France
	Urin. bladder	<i>Myxidium lieberkuhni</i>	France, Germany
<i>Lucioperca lucioperca</i> L ( <i>L. sandra</i> Cuv.)	"	<i>Sphaerospora elegans</i>	Germany
	Branchiae	<i>Henneguya acerinae</i>	" , Austria
	" , head, fin, opercle	<i>Myxobolus</i> sp	?
	"	<i>Henneguya gigantea</i>	Aus , Serbia
	"	Gen. et sp. incert.	Austria
<i>L. volgensis</i> Pall	Muscle	<i>Myxobolus sandrae</i>	Russia
	Branchiae, cor- nea, dorsal fin	<i>volgensis</i>	"
<i>Melanogrammus aeglefinis</i>	Gall-bladder	<i>Myxidium bergense</i>	Canada
<i>Menticirrhus americanus</i> L	"	<i>striatum</i>	Brazil
<i>Merluccius merluccius</i> L. ( <i>M. vulgaris</i> )	"	<i>Ceratomyxa globulifera</i>	France
	"	<i>Leptotheca elongata</i>	" , Italy
	"	Gen incert <i>merluccii</i>	Italy
	"	<i>Ceratomyxa aggregata</i>	U. S. A.
<i>Micropogon undulatus</i>	Urin Bladder	<i>Henneguya microspora</i>	U. S. A
<i>Micropterus salmoides</i> Lac			
<i>Misgurnus anguillicaudatus</i> Cantor	Branchiae	<i>Myxobolus</i> sp	Nippon
	Gall-bladder	<i>Chloromyxum fujitai</i>	"
	"	<i>misgurni</i>	"
	"	<i>Myxidium kagayamai</i>	"
	"	<i>Myxobolus misgurni</i>	"
<i>Molva vulgaris</i> Flem	Bone	<i>aeglefini</i>	Austria
	Gall-bladder	<i>Leptotheca informis</i>	Norway
<i>Motella maculata</i> Risso	"	<i>Sphaeromyxa hellandi</i>	"
	"	<i>balbiani</i>	France
	"	<i>Ceratomyxa arcuata</i>	"
	"	<i>Leptotheca elongata</i>	" , Monaco
	"	<i>Sphaeromyxa balbianii</i>	France
<i>M. tricirrata</i> Bl	"	<i>sabrazesi</i>	Monaco
<i>Mugil auratus</i> Risso	Intestine, stom- ach, spleen, pyloric coecum	<i>Myxobolus mulleri</i>	Italy
<i>M. capito</i> Cuv	Kidney	<i>exiguus</i>	" , France
	"	<i>exiguus</i>	"
<i>M. cephalus</i> L	Gall-bladder	<i>Myxidium incurvatum</i>	U. S. A.
<i>M. chelo</i> Cuv	Stomach, spleen, kidney, etc.		Italy,
		<i>Myxobolus exiguus</i>	France

Host	Organ Infected	Myxosporidian	Locality
<i>M. sp.</i> .....	Kidney	<i>Sphaerospora rostrata</i>	Italy, France
<i>Muraena sp.</i> .....	Gall-bladder	<i>Ceratomyxa sp.</i>	Monaco
<i>Mustelus canis</i> Mitch. ( <i>M. vulgaris</i> ).....	Gall-bladder	<i>Ceratomyxa sphaerulosa</i>	France
<i>Nerophis aequoreus</i> L.....	Gall-bladder	<i>Myxidium incurvatum</i>	France
	Muscle	<i>Chloromyxum quadratum</i>	"
<i>N. annulatus</i> .....	Gall-bladder	<i>Myxidium incurvatum</i>	"
	"	<i>Sphaeromyxa sabraesi</i>	Monaco
<i>N. lumbriciformis</i> .....	"	<i>Myxidium incurvatum</i>	France
<i>Notropis megalops</i> Raf.....	Subcut. tissue	Gen. et spec. incert.	U. S. A.
<i>N. gilberti</i> J. et M.....	Muscle	<i>Myxobolus orbiculatus</i>	U. S. A.
<i>N. bleinnius</i> .....	"	"	"
<i>N. anogenus</i> .....	Fins	<i>aureatus</i>	"
	"	<i>Henneguya brachyura</i>	"
<i>Oncorhynchus keta</i> .....	Under the skin	<i>Henneguya salminicola</i>	Kamtschatka
<i>O. kisutch</i> .....	"	"	"
	Connective tiss. of body muscle	"	Alaska
<i>O. nerka</i> .....	Gall-bladder	<i>Chloromyxum wardi</i>	"
<i>Ophidium vasalli</i> .....	Gall-bladder	<i>Ceratomyxa arcuata</i>	Monaco
<i>Opsanus tau</i> .....	Urin. bladder	<i>Sphaerospora polymorpha</i>	U. S. A.
<i>Pagellus centrodontus</i> Del....	Gall-bladder	<i>Ceratomyxa arcuata</i>	France, Italy
<i>Paralichthys albiguttus</i> J. et G.....	Urin. bladder	<i>navicularia</i>	U. S. A.
	"	<i>spinosa</i>	"
	"	<i>Leptotheca glomerosa</i>	"
	"	<i>Sinuolinea brachiophora</i>	"
	"	<i>capsularis</i>	"
	"	<i>opacila</i>	"
<i>P. dentatus</i> .....	Gall-bladder	<i>Ceratomyxa drepanopsellae</i>	"
	Urin. bladder	<i>navicularia</i>	"
	"	<i>Leptotheca lobosa</i>	"
	"	<i>Sinuolinea capsularis</i>	"
<i>Parasilurus asotus</i> L.....	Intestinal wall	<i>Myxobolus miyairii</i>	Nippon
<i>Petrius alepidotus</i> .....	Gall-bladder	<i>Ceratomyxa monospora</i>	U. S. A.
<i>Perca flavescens</i> .....	Spleen	<i>Myxobolus sp.</i>	"
	Urin. bladder	<i>Henneguya wisconsinensis</i>	"
<i>P. fluviatilis</i> .....	Branchiae	<i>texta</i>	Italy, Germany
	"	<i>Henneguya minuta</i>	"
	"	<i>Myxobolus sp.</i>	Germany
	" , operculum	<i>permagnus</i>	"
	"	<i>Myxosoma dujardini</i>	Switzerland
	"	<i>Henneguya psorospermica</i>	"
<i>Phoxinus (Clinostomus)</i> <i>funduloides</i> Girard	Under scales on ext. surf.	<i>Myxobolus transovalis</i>	U. S. A.
<i>P. laevis</i> .....	Branchiae	<i>mülleri</i>	France

Host	Organ Infected	Myxosporidian	Locality
<i>P. laevis</i>	Kidney, ovary	<i>Myxidium histophilum</i>	France
	Urin. bladder	<i>Sphaerospora elegans</i>	Germany
<i>Phycis blennioides</i> Br	Urin. bladder	<i>Zschokkella hildae</i>	Norway
<i>P. mediterraneus</i> ( <i>P. phycis</i> L.)	Gall-bladder	<i>Leptotheca polymorpha</i>	France
<i>Pimelodus sebae</i> Cuv. et Val	Membrane lining branchial cavity	<i>Henneguya linearis</i>	S. America
<i>Pimephales notatus</i> Raf	Gall-bladder	<i>Myxobolus notatus</i>	Canada
<i>Piramutana blochi</i> C. et V.	?	<i>inaequalis</i>	S. America
<i>Platystoma fasciatum</i> L	Branchiae	<i>Henneguya linearis</i>	"
<i>Pleuronectes flesus</i> L	Gall-bladder	? <i>Ceratomyxa drepanopsettae</i>	Norway
<i>P. platessa</i> L	"	"	"
	Otic-capsule	<i>Sphaerospora platessae</i>	England
<i>Pomolobus aestivalis</i>	Muscle	<i>Chloromyxum clupeidae</i>	U. S. A.
<i>P. mediocris</i> Mitch	"	<i>clupeidae</i>	"
<i>P. pseudoharengus</i> Young	"	<i>clupeidae</i>	"
<i>Pseudopleuronectes americanus</i>	Gall-bladder	<i>Ceratomyxa acadensis</i>	Canada
	"	<i>Myxidium</i> sp.	"
	Subcutaneous muscl. tissue	<i>Myxobolus pleuronectidae</i>	U. S. A.
<i>Pteroplatea maclura</i> Le Sueur	Gall-bladder	<i>Chloromyxum leydigi</i>	"
	"	<i>Leptotheca scissura</i>	"
<i>Raja asterias</i>	"	<i>Myxidium giganteum</i>	Italy
<i>R. batis</i> L	"	<i>Chloromyxum leydigi</i>	France
	Gall-duct	<i>Myxidium</i> sp.	Germany ?
<i>R. radiata</i>	Gall-bladder	<i>Chloromyxum</i> sp.	Murman Coast
<i>R. clavata</i> L	"	<i>Chloromyxum leydigi</i>	France
<i>R. undulata</i> Lac	"	<i>Chloromyxum leydigi</i>	"
<i>Rhina squatina</i> L	"	<i>Chloromyxum leydigi</i>	France, Germany
<i>Rhinobathus</i> sp. (?) Awer	"	<i>Ceratomyxa</i> sp. (?)	Africa
<i>Rhodeus amarus</i> Bl	Branchiae	<i>Myxobolus cycloides</i>	Germany
<i>Salmo fontinalis</i> Mitch	Cartilage, perichondrium	<i>Lentospora cerebralis</i>	"
<i>Scardinius erythrophthalmus</i> . . .	Branchiae	<i>Myxobolus cycloides</i>	"
	"	<i>scardinii</i>	Russia
	"	<i>Myxosoma dujardini</i>	France, Germany
	Gall-bladder	<i>Myxidium macrocapsulare</i>	"
	Muscle, spleen	<i>Myxobolus dispar</i>	France
	Air-bladder	<i>permagnus</i>	Germany
	"	<i>physophilus</i>	Russia
<i>Scatophagus argus</i>	Gall-bladder	<i>Ceratomyxa</i> sp. (?)	Africa

Host	Organ Infected	Myxosporidian	Locality
<i>Scoliodon tetrarhynchos</i>	Gall-bladder	<i>Ceratomyxa abbreviata</i>	U. S. A.
	"	<i>attenuata</i>	"
	"	<i>sphaerophora</i>	"
	"	<i>'taenia</i>	"
	"	<i>Chloromyxum leydigi</i>	"
<i>Scomber scombrus</i> L.	"	<i>Leptotheca parva</i>	France, Norway
	Kidney	<i>renicola</i>	France
	?	Gen. et sp. inc.	Germany?
<i>Scorpaena porcus</i> L.	Gall-bladder	<i>Ceratomyxa arcuata</i>	France
<i>S. scrofa</i> L.	"	<i>Ceratomyxa arcuata</i>	"
	"	<i>Myxidium incurvatum</i>	"
<i>S. sp</i>	"	<i>Leptotheca agilis</i>	" , Germany
<i>Scyllium canicula</i>	"	<i>Ceratomyxa sphaerulosa</i>	Monaco
	"	<i>Chloromyxum leydigi</i>	" , France
			Germany
<i>S. asterias</i>	"	"	Italy
<i>Sebastes dactylopterus</i>	"	<i>Leptotheca macrospora</i>	Norway
<i>S. norvegicus</i>	"	<i>Leptotheca sp.</i>	Eastern Finmark
<i>S. viviparus</i> H. Kr.	"	<i>Leptotheca macrospora</i>	Norway
<i>Siphonostoma rondeletii</i>	"	<i>Sphaeromyxa sabralesi</i>	Monaco
<i>Siphostoma floridae</i>	"	<i>balbianii</i>	U. S. A.
	Urin. bladder	<i>Sinuolinea arborescens</i>	"
<i>S. louisianae</i>	Gall-bladder	<i>Sphaeromyxa balbianii</i>	"
<i>Solea vulgaris</i>	"	<i>Myxidium gadi</i>	France
<i>Sparus berda</i>	"	<i>Ceratomyxa (?) spari</i>	Africa
<i>Sphaeroides maculatus</i>	Urin. bladder	<i>navicularia</i>	U. S. A.
	"	<i>Sinuolinea capsularis</i>	"
	"	<i>Zschokkella globulosa</i>	"
<i>Spinax spinax</i> L.	Gall-bladder	<i>Chloromyxum leydigi</i>	Italy, France
<i>Squalis agassizii</i> Heck	Branchiae	<i>Myxobolus mulleri</i>	France
<i>S. a. Savigny</i> Bona- parte	"	<i>Myxobolus mulleri</i>	"
<i>Stenotomus chrysops</i> L.	Muscle	<i>Chloromyxum clupeiidae</i>	U. S. A.
<i>Stizostedion vitreum</i> Mitch.	Urin. bladder	Gen. et sp. incert.	Canada
<i>Syngnathus acus</i> L.	Gall-bladder	<i>Myxidium incurvatum</i>	France
	"	<i>Sphaeromyxa sabralesi</i>	Italy, Monaco
	Muscle	<i>Chloromyxum quadratum</i>	France
<i>S. typhle</i>	Gall-bladder	<i>Myxidium incurvatum</i>	France
<i>Synodontis schall</i> Bl. Schn	Integum. of cephalic reg.	<i>Henneguya strongylura</i>	Egypt
	?	<i>Myxobolus inaequalis</i>	S. America
<i>Synodus faetans</i>	Gall-bladder	<i>Ceratomyxa agglomerata</i>	U. S. A.
	"	<i>amorpha</i>	"
<i>Tautoglabrus adspersus</i> Walb.	Muscle	<i>Chloromyxum clupeiidae</i>	"

Host	Organ Infected	Myxosporidian	Locality
<i>Thymallus thymallus</i> L	Gall-bladder	<i>Chloromyxum thymalli</i>	Austria
	"	<i>Myxobolus</i> sp.	"
	Neurilemma (?)	<i>pfeifferi</i>	Germany ?
<i>Thysanophrys japonicus</i>	Gall-bladder	<i>Sphaeromyxa exneri</i>	Africa
<i>Tinca tinca</i> L. ( <i>T. vulgaris</i> )	Branchiae	<i>Myxobolus piriformis</i>	France, Germany
	Air-bladder, kidney, etc.	<i>ellipsoides</i>	"
	Gall-bladder	<i>Chloromyxum cristatum</i>	France
	"	<i>Myxidium pfeifferi</i>	Germany
	Kidney	<i>Myxobolus cyprini</i>	Germany, Hungary
<i>Torpedo narce</i> Risso	Gall-bladder	<i>Chloromyxum leydsi</i>	France
<i>T. ocellata</i>	"	<i>Chloromyxum leydsi</i>	Germany
<i>T. torpedo</i> L	"	<i>Chloromyxum leydsi</i>	"
<i>Trachinus draco</i> L	"	<i>Ceratomyxa reticularis</i>	"
	"	<i>Myxidium incurvatum</i>	"
<i>Trachurus trachurus</i> L	Muscle	<i>Chloromyxum quadratum</i>	France, Germany
<i>Trutta fario</i> L	Gall-bladder, Gall-duct	<i>Chloromyxum truttae</i>	France
	Nervous syst.	<i>Myxobolus neurobius</i>	Germany
	Subcutaneous conn. tiss. at base of fin	<i>Henneguya nusslii</i>	"
<i>T. iridea</i> Gibb	Cartilage, peri- chondrium	<i>Lentospora cerebralis</i>	"
<i>T. salar</i> L	"	"	"
	Gall-bladder	<i>Myxidium oviforme</i>	Norway
<i>Trygon pastinaca</i> L	Gall-bladder	<i>Chloromyxum leydsi</i>	France
	"	<i>Leptotheca agilis</i>	" , Italy
<i>Tylosurus marianus</i>	Urin bladder	<i>Chloromyxum granulosum</i>	U S. A.
<i>T. schismatorhynchus</i>	Gall-bladder	<i>Ceratomyxa tylosuri</i>	Africa
<i>Urophycis chuss</i>	"	<i>acadiensis</i>	Canada
<i>Zoarces angularis</i>	"	<i>acadiensis</i>	"
<b>Amphibia</b>			
<i>Bufo lentiginosus</i>	Kidney	<i>Wardia ohlmacheri</i>	U. S. A
<i>B. marinus</i> L	Gall-bladder	<i>Sphaeromyxa immersa</i>	Brazil
<i>Hyla aurea</i>	Testis, ovary	<i>Myxobolus hylae</i>	Australia
<i>Leptodactylus ocellatus</i>	Gall-bladder	<i>Sphaeromyxa immersa</i>	Brazil
<i>Molge cristata</i> Laur. ( <i>Triton</i> c.)	"	<i>Chloromyxum caudatum</i>	France
<i>Proteus anguineus</i> L	Kidney	<i>Chloromyxum protei</i>	Austria
<i>Rana esculenta</i>	"	? <i>Wardia ohlmacheri</i>	France ?
<i>R. temporaria</i> ( <i>R. fusca</i> )	"	? <i>Wardia ohlmacheri</i>	"
<b>Reptilia</b>			
<i>Emys orbicularis</i> L. ( <i>Cistudo europaea</i> )	Kidney	<i>Myxidium danilewskyi</i>	Russia, France

Host	Organ Infected	Myxosporidian	Locality
<i>Lacerta</i> sp.....	Ovarian egg	Gen. et spec. incert.	Italy
<i>Trionyx (Amyda) gangetica</i> .....	Kidney	<i>Myxidium mackiei</i>	India
<i>T. spinifera</i> .....	"	<i>americanum</i>	U. S. A.

### C. DISTRIBUTION OF MYXOSPORIDIA IN THE ORGANS OF THE HOST

Altho some species are found in various organs of the host animal, the majority has one or two particular seats of infection. Among the various organs which become infected, the gall-bladder is most frequently infected. The kidney, branchia and urinary bladder have less chances of being parasitized. As to the infection of the reproductive organs of the host, little is known. The male reproductive organ becomes rarely infected, being reported only twice. The female reproductive organ, however, is more frequently infected. The infection of the next generation of the host animal thru the infected ovum which is known to occur in some Microsporidian parasites, has not been reported in Myxosporidia as yet.

### LIST IV. ORGANS OF HOST INFECTED BY MYXOSPORIDIA

#### I. PISCES

- 1) Integument.—*Sphaerospora* sp. Southwell et Prashad (under the scales)
  - Myxobolus seni* Southwell et Prashad (fin)
  - Myxobolus transovalis* Gurley (under the scales)
  - Myxobolus unicapsulatus* Gurley (head)
  - Myxobolus cycloides* Gurley (opercle)
  - Myxobolus inaequalis* Gurley (head)
  - Myxobolus* sp. Gurley (opercle, head, fin)
  - Myxobolus squamae* Keysseltz (inner surface of the scales)
  - Myxobolus volgensis* Reuss (fin)
  - Myxobolus permagnus* Wegener (operculum)
  - Myxobolus aureatus* Ward (fin)
  - Henneguya brachyura* Ward (fin-ray)
  - Henneguya linearis* (Gurley) Labbé (membrane lining branchial cavity)
  - Henneguya gurleyi* Kudo (base of spines of dorsal fin)
  - Henneguya strongylura* (Gurley) Labbé (cephalic region)
  - Lentospora dermatobia* Ishii
- 2) Connective tissue.—*Myxidium anguillae* Ishii (subcutaneous)
  - Myxobolus fuhrmanni* Auerbach (under the oral mucous membrane)
  - Myxobolus oviformis* Thélohan (subcutaneous)
  - Myxobolus lintoni* Gurley (subcutaneous)
  - Myxobolus oblongus* Gurley (chiefly of the head)
  - Myxobolus gigas* Auerbach (of operculum, sides and fins)
  - Myxobolus capsulatus* Davis (visceral)
  - Henneguya kolesnikovi* (Gurley) Labbé (interstitial)
  - Henneguya nüsslii* Schuberg et Schröder (at the base of dorsal fin)
  - Henneguya miyairii* Kudo (of the head)
  - Gen. et sp. incert. Linton (subcutaneous)



- 3) Muscle.—*Leptotheca perata* (Gurley) Labbé  
*Chloromyxum quadratum* Thélohan  
*Chloromyxum funduli* Hahn  
*Chloromyxum clupeiidae* Hahn  
*Lentospora multiplicata* Reuss  
*Myxobolus notatus* Mavor (connective tissue of voluntary muscle)  
*Myxobolus pfeifferi* Thélohan  
*Myxobolus sandrae* Reuss  
*Myxobolus musculi* Keysselitz  
*Myxobolus funduli* Kudo  
*Myxobolus pleuronectidae* Hahn  
*Myxobolus* sp. Southwell (subcutaneous intermuscular tissue)  
*Myxobolus nodularis* Southwell et Prashad  
*Myxobolus orbiculatus* Kudo  
*Henneguya creplini* (Gurley) Labbé  
*Henneguya monura* (Gurley) Labbé  
*Henneguya zschokkei* (Gurley) Doflein  
*Henneguya salminicola* Ward  
 Gen. et spec. incert. Leydig
- 4) Eye.—*Sphaerospora platessae* Woodcock (optic capsule)  
*Myxobolus oculi-leucisci* Trojan (vitreous body)  
*Myxobolus ellipsoides* Thélohan  
*Myxobolus mülleri* Bütschli  
*Myxobolus aeglefini* Auerbach  
*Myxobolus volgensis* Reuss  
*Myxobolus magnus* Awerinzew  
*Henneguya schizura* (Gurley) Labbé (intercellular tissue of eye muscle)
- 5) Branchiae.—*Sphaerospora carassii* Kudo  
*Myxosoma dujardini* Thélohan  
*Myxosoma* (?) *lobatum* Nemeček  
*Myxosoma funduli* Kudo  
*Lentospora acula* (Fujita)  
*Myxobolus piriformis* Thélohan  
*Myxobolus toyamai* Kudo  
*Myxobolus rohilaie* Southwell et Prashad  
*Myxobolus dispar* Thélohan  
*Myxobolus ellipsoides* Thélohan  
*Myxobolus exiguus* Thélohan  
*Myxobolus oviformis* Thélohan  
*Myxobolus mülleri* Bütschli  
*Myxobolus globosus* Gurley  
*Myxobolus cycloides* Gurley (also pseudobranchiae)  
*Myxobolus sphaeralis* Gurley  
*Myxobolus anurus* Cohn  
*Myxobolus* sp. Gurley  
*Myxobolus gigas* Auerbach  
*Myxobolus volgensis* Reuss  
*Myxobolus scardinii* Reuss  
*Myxobolus macrocapsularis* Reuss  
*Myxobolus bramae* Reuss  
*Myxobolus cyprinicola* Reuss

*Myxobolus balleri* Reuss  
*Myxobolus* sp. Miyairi  
*Myxobolus* sp. Wegener  
*Myxobolus permagnus* Wegener  
*Myxobolus rotundus* Nemeček  
*Myxobolus minutus* Nemeček  
*Myxobolus funduli* Kudo  
*Myxobolus koi* Kudo  
*Myxobolus discrepans* Kudo  
*Henneguya psorospermica* Thélohan  
*Henneguya texta* (Cohn)  
*Henneguya minuta* (Cohn)  
*Henneguya lobosa* (Cohn)  
*Henneguya creplini* (Gurley) Labbé  
*Henneguya linearis* (Gurley) Labbé  
*Henneguya acerinae* Schröder  
*Henneguya gigantea* Nemeček  
 Gen. et spec. incert. Heckel et Kner

- 6) Heart.—*Myxobolus cordis* Keysseltz (muscle of ventricle and bulbus arteriosus)  
 Gen. et spec. incert. Leydig (auriculo-ventricular valve)
- 7) Air bladder.—*Myxobolus ellipsoides* Thélohan (conn. tiss.)  
*Myxobolus mülleri* Bütschli (conn. tiss.)  
*Myxobolus physophilus* Reuss (surface)  
*Myxobolus permagnus* Wegener
- 8) Body-cavity (cyst).—*Myxobolus* sp. Gurley  
*Myxobolus carassii* Klokacewa  
 Gen. et spec. incert. Leydig
- 9) Nervous tissue.—*Myxobolus neurobius* Schuberg et Schröder  
*Lentospora encephalina* Mulsow (blood vessel of brain)
- 10) Bone, cartilage, perichondrium.—*Lentospora cerebralis* (Hofer) Plehn  
*Myxobolus aeglegini* Auerbach  
*Henneguya brachyura* Ward (of fin)
- 11) Stomach, pyloric cecum.—*Myxobolus exiguus* Thélohan  
*Myxobolus mesentericus* Kudo  
*Henneguya tenuis* Vaney et Conte
- 12) Liver.—*Myxobolus ellipsoides* Thélohan  
*Myxobolus oviformis* Thélohan  
*Myxobolus cyprini* Dofflein  
*Myxobolus cordis* Keysseltz  
*Myxobolus musculi* Keysseltz  
*Myxobolus carassii* Klokacewa  
*Myxobolus mesentericus* Kudo
- 13) Gall-bladder.—*Leptotheca agilis* Thélohan  
*Leptotheca elongata* Thélohan  
*Leptotheca polymorpha* (Thélohan) Labbé  
*Leptotheca parva* Thélohan  
*Leptotheca hepseti* Thélohan  
*Leptotheca* sp. Awerinzew  
*Leptotheca macrospora* Auerbach  
*Leptotheca informis* Auerbach  
*Leptotheca longipes* Auerbach

*Leptotheca fusiformis* Davis  
*Leptotheca scissura* Davis  
*Ceratomyxa arcuata* Thélohan  
*Ceratomyxa sphaerulosa* Thélohan  
*Ceratomyxa pallida* Thélohan  
*Ceratomyxa globurifera* Thélohan  
*Ceratomyxa appendiculata* Thélohan  
*Ceratomyxa truncata* Thélohan  
*Ceratomyxa reticularis* Thélohan  
*Ceratomyxa inaequalis* Doflein  
*Ceratomyxa linospora* Doflein  
*Ceratomyxa ramosa* Awerinzew  
*Ceratomyxa drepanopsellae* Awerinzew  
*Ceratomyxa tylosuri* Awerinzew  
*Ceratomyxa* (?) *spari* Awerinzew  
*Ceratomyxa* sp. (?). Awerinzew  
*Ceratomyxa* sp (?). Awerinzew  
*Ceratomyxa acadensis* Mavor  
*Ceratomyxa* sp. Georgévitch  
*Ceratomyxa coris* Georgévitch  
*Ceratomyxa herouardi* Georgévitch  
*Ceratomyxa mesospora* Davis  
*Ceratomyxa sphairophora* Davis  
*Ceratomyxa taenia* Davis  
*Ceratomyxa attenuata* Davis  
*Ceratomyxa recurvata* Davis  
*Ceratomyxa lunata* Davis  
*Ceratomyxa abbreviata* Davis  
*Ceratomyxa flagellifera* Davis  
*Ceratomyxa agglomerata* Davis  
*Ceratomyxa amorphia* Davis  
*Ceratomyxa monospora* Davis  
*Ceratomyxa streptospora* Davis  
*Ceratomyxa aggregata* Davis  
*Ceratomyxa undulata* Davis  
*Chloromyxum leydigi* Mingazzini  
*Chloromyxum fluviatile* Thélohan  
*Chloromyxum truttiae* Léger (also gall-duct)  
*Chloromyxum cristatum* Léger  
*Chloromyxum dubium* Auerbach  
*Chloromyxum* sp. Awerinzew  
*Chloromyxum thymalli* Lebzelter  
*Chloromyxum koi* Fujita  
*Chloromyxum magnum* Awerinzew  
*Chloromyxum misgurni* Kudo  
*Chloromyxum fujitai* Kudo  
*Chloromyxum trijugum* Kudo  
*Chloromyxum catostomi* Kudo  
*Chloromyxum wardi* Kudo  
*Sphaerospora masovica* Cohn  
*Myxidium incurvatum* Thélohan  
*Myxidium sphaericum* Thélohan

*Myxidium* sp. Gurley (only in gall-duct)  
*Myxidium giganteum* Doflein  
*Myxidium pfeifferi* Auerbach  
*Myxidium instatum* Auerbach  
*Myxidium bergense* Auerbach  
*Myxidium procerum* Auerbach  
*Myxidium macrocapsulare* Auerbach  
*Myxidium* sp. Awerinzew  
*Myxidium oviforme* Pariai  
*Myxidium* sp. Mavor  
*Myxidium kagayamai* Kudo  
*Myxidium gadi* Georgévitch  
*Myxidium glutinosum* Davis  
*Myxidium phyllium* Davis  
*Myxidium striatum* Cunha et Fonseca  
*Myxobolus misgurni* Kudo (few spores only)  
*Myxobolus* sp. Lebzelter (spores only)  
*Sphaeromyxa balbianii* Thélohan  
*Sphaeromyxa incurvata* Doflein  
*Sphaeromyxa sabrazesi* Laveran et Mesnil  
*Sphaeromyxa hellandi* Auerbach  
*Sphaeromyxa exneri* Awerinzew  
*Sphaeromyxa gasterostei* Georgévitch  
*Zschokkella nova* Klokacewa  
*Zschokkella acheilognathi* Kudo (also in gall-duct)  
 Gen. incert. *congrui* Perugia  
 Gen. incert. *merlucii* Perugia  
 Gen. et spec. incert. Mavor

- 14) Spleen.—*Myxobolus piriformis* Thélohan  
*Myxobolus* sp. Kudo  
*Myxobolus ellipsoides* Thélohan  
*Myxobolus exiguus* Thélohan  
*Myxobolus oviformis* Thélohan  
*Myxobolus pfeifferi* Thélohan  
*Myxobolus cyprini* Doflein  
*Myxobolus cordis* Keysselitz  
*Myxobolus musculi* Keysselitz  
*Myxobolus mesentericus* Kudo  
 15) Intestine.—*Myxobolus exiguus* Thélohan  
*Myxobolus mülleri* Bütschli  
*Myxobolus pfeifferi* Thélohan  
*Myxobolus miyairii* Kudo  
*Myxobolus carassii* Klokacewa  
*Myxobolus mesentericus* Kudo  
*Henneguya peri-intestinalis* Cépède  
*Henneguya tenuis* Vaney et Conte  
 16) Ovary.—*Wardia ovinocua* Kudo  
*Sphaerospora elegans* Thélohan  
*Myxidium histophilum* Thélohan  
*Myxobolus pfeifferi* Thélohan  
*Myxobolus mülleri* Bütschli  
*Myxobolus musculi* Keysselitz

*Henneguya oviperda* (Cohn)

*Henneguya media* Thélohan

*Henneguya brevis* Thélohan

17) Kidney.—a) Urinary tubules.—*Leptotheca renicola* Thélohan

*Mitraspora caudata* (Parisi) Kudo

*Mitraspora cyprini* Fujita (also in ureter)

*Mitraspora elongata* Kudo

*Sphaerospora elegans* Thélohan

*Sphaerospora divergens* Thélohan

*Henneguya media* Thélohan

*Henneguya brevis* Thélohan

*Henneguya gasterostei* Parisi

*Hoferellus cyprini* Doflein

b) Tissue.—*Mitraspora elongata* Kudo

*Chloromyxum quadratum* Thélohan

*Sphaerospora rostrata* Thélohan (Malpighian bodies)

*Myxidium histophilum* Thélohan

*Lentospora asymmetrica* Parisi

*Myxobolus pfeifferi* Thélohan

*Myxobolus cyprini* Doflein

*Henneguya neapolitana* Parisi (conn. tiss. of ren. tubules)

*Hoferellus cyprini* Doflein

c) Seat, unstated.—*Chloromyxum mucronatum* Gurley

*Sphaerospora angulata* Fujita

*Myxidium barbatulae* Cépède

*Myxidium giardi* Cépède

*Myxobolus piriformis* Thélohan

*Myxobolus ellipsoides* Thélohan

*Myxobolus exiguus* Thélohan

*Myxobolus oviformis* Thélohan

*Myxobolus mülleri* Bütschli

*Myxobolus obesus* Gurley

*Myxobolus cycloides* Gurley

*Myxobolus cordis* Keysselitz

*Myxobolus musculi* Keysselitz

18) Urinary bladder.—*Leptotheca lobosa* Davis

*Leptotheca glomerata* Davis

*Ceratomyxa navicularia* Davis

*Ceratomyxa spinosa* Davis

*Chloromyxum mucronatum* Gurley

*Chloromyxum granulosum* Davis

*Sphaerospora elegans* Thélohan

*Sphaerospora divergens* Thélohan

*Sphaerospora polymorpha* Davis

*Sphaerospora* sp. Davis

*Sinuolinea dimorpha* Davis (also in ureter)

*Sinuolinea capsularis* Davis

*Sinuolinea arborescens* Davis

*Sinuolinea opacita* Davis

*Sinuolinea brachiophora* Davis

*Myxidium lieberkühni* Bütschli

*Zschokkella hildae* Auerbach

*Zschokkella globulosa* Davis

*Myxoproteus ambiguus* (Thélohan) Doflein*Myxoproteus cordiformis* Davis*Myxoproteus cornutus* Davis*Henneguya legeri* Cépède*Henneguya wisconsinensis* Mavor et Strasser*Henneguya miclospora* Kudo

Gen. et spec. incert. Mavor

19) Testis.—*Myxobolus pfeifferi* Thélohan (only spores)20) Mesentery.—*Myxobolus mesentericus* Kudo21) Seat unknown.—*Henneguya* sp. Gurley (integument?)

Gen. et. spec. incert. Borne

## II AMPHIBIA

1) Gall-bladder.—*Chloromyxum caudatum* Thélohan*Sphaeromyxa immersa* (Lutz) Thélohan2) Urinary tubules of kidney.—*Wardia ohlmacheri* (Gurley) Kudo*Chloromyxum protei* Joseph

TABLE I

	Integument	Conn. tissue	Muscle	Eye	Gill	Heart	Air bladd	Nerv. tiss.	Bone, cartilage	Stomach wall	Liver	Gall bladd	Spleen	Intestine wall	Testis	Ovary	Kidney	Body cav.	Urinary bladder	Mesentery	Seat unknown
Leptotheca			1									11					1(a)*		2		
Ceratomyxa												33							2		
Myxoproteus																1	1(a)		3		
Wardia																	3(a)				
Mitraspora																	1(b)*				
Chloromyxum			3									14					1(a)				
																	1(b)				
																	1(c)*	1	2		
Sphaerospora	1			1	1							1				1	2(a)				
																	1(b)				
																	1(c)		4		
Sinuolinea																	2(a)		5		
Myxidium		1										18				1	1(b)				
																	2(c)				
																	3(a)		1		
Sphaeromyxa	...											7									
Zschokkella												2							2		
Myxosoma					3																
Lentospora	1		1	1				1	1								1(b)	1			
Myxobolus	10	6	9	6	28	1	4	1	1	2	7	2	10	6	2	4	2(b)				
																	9(c)	1		1	1
Henneguya	4	3	4	1	8				1	1				2	3		3(a)		3		1
																	1(b)				
Hioferellus																	1(a)				
																	1(b)				
Total	16	10	18	8	41	1	4	2	3	3	7	8	10	8	2	10	39	3	24	1	2

\* For (a), (b) and (c), see page 42

3) Testis, oviduct.—*Myxobolus kyllae* Johnston et Bancroft

### III REPTILIA

1) Kidney (ren. tub.).—*Myxidium danilewskyi* Laveran

*Myxidium mackiei* Bosanquet

*Myxidium americanum* Kudo

2) Ovary—Gen et spec incert. Mingazzini

### IV INSECTA

1) Abdominal cavity.—*Chloromyxum diploxyis* Gurley

### V ANNELIDA

*Myxobolus* sp Gurley

The data in this section are summarized on the preceding page (Table I).

## D THE EFFECT OF ENVIRONMENT ON THE ORGANEL DISTRIBUTION OF MYXOSPORIDIA IN HOSTS

Myxosporidia are almost equally distributed among marine and fresh-water fishes in regard to the number of species. This is shown in the following table.

TABLE II

Genus	Number of species found in marine fish	Number of species found in fresh-water fish	Other hosts			
			Rept	Amph	Insect	Annelida
Leptotheca (15)*	15					
Ceratomyxa (35)	35					
Myxoproteus (3)	3					
Wardia (2)		1		1		
Mitraspora (3)		3				
Chloromyxum (22)	7	12		2	1	
Sphaerospora (10)	5	5				
Sinuolinea (5)	5					
Myxidium (26)	17	8	3			
	(2 common)	(2 common)				
Sphaeromyxa (7)	6			1		
Zschokkella (4)	2	2				
Myxosoma (3)	1	2				
Lentospora (6)	2	6				
	(2 common)	(2 common)				
Myxobolus (63)	5	56		1		1
Henneguya (32)	1	31				
Hoferellus (1)		1				
Gen. et spec. incert (12)	4	7	1			
TOTAL 237+12	104+4	134+7	4	5	1	1

\* The number in parenthesis denotes the number of species in the corresponding genus.

These genera have certain relations to the organal distribution in the body of the host, which are shown in List IV (page 37) and Table I (on page 43) and which can be put together as follows:

TABLE III

Genus	Number of species found in body-cavity	Number of species found in tissue	Number of species found in both	Seat unknown
Leptotheca (15)	14	1		.
Ceratomyxa (35)	35			
Myxoproteus (3)	3			
Wardia (2)	1	1		
Mitraspora (3)	2		1	
Chloromyxum (22)	18	4		
Sphaerospora (10)	4	4	1	1
Sinuolinea (5)	5			
Myxidium (26)	22	4		
Sphaeromyxa (7)	6			1
Zschokkella (4)	4			
Myxosoma (3)		3		
Lentospora (6)	1	5		
Myxobolus (63)	2	59		2
Henneguya (32)	4	28		
Hoferellus (1)			1	
Gen. et spec. inct (12)	4	5		3
TOTAL 237+12	121+4	109+5	3	4+3

From the facts shown in the above tables, the following conclusions can be drawn.

1) The genera *Leptotheca* (one species in tissue), *Ceratomyxa*, *Myxoproteus*, *Sinuolinea* and *Sphaeromyxa* (one species in Amphibia) include parasites from the body cavity of marine fish.

2) The majority of the genera *Lentospora*, *Myxosoma*, *Myxobolus* (one species in Amphibia), *Henneguya* and *Hoferellus* include parasites in tissues of fresh-water fish.

3) The genera *Chloromyxum*, *Sphaerospora*, *Myxidium* and *Zschokkella* include forms that infect the body-cavity as well as the tissue of marine and fresh-water fishes.

4) The genus *Mitraspora* includes three species that parasitize the fresh-water fish.

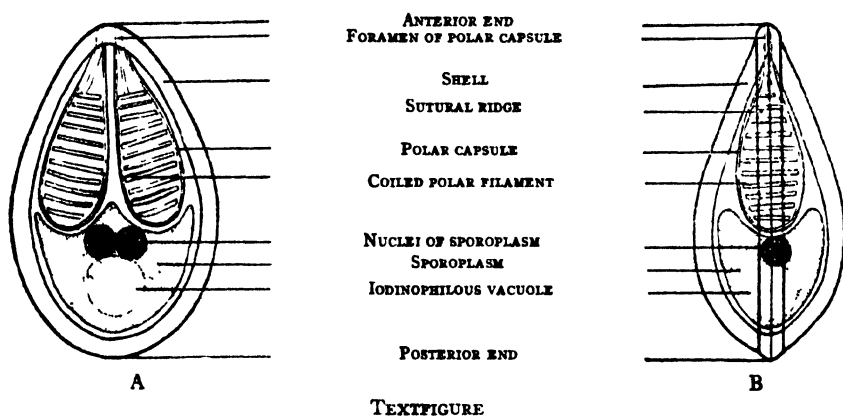
5) The genus *Myxidium* has three species found in the kidney of reptiles.



- 6) The genera *Wardia*, *Chloromyxum*, *Sphaeromyxa* and *Myxobolus* include species parasitic in Amphibia.
- 7) The genus *Chloromyxum* has one species found in an insect.
- 8) The genus *Myxobolus* has one species found in an annelid, which was not normally recorded.

## THE SPORE

As will be shown later (page 52-55), the spore stage is still the only constant character by which various forms of Myxosporidia are identified from each other. For this reason it is necessary to have a clear conception of the form and structure of the spore and at the same time to define the terms used in the present paper, even tho they have commonly been used heretofore.



TEXTFIGURE  
 DIAGRAMMATICAL FRONT [A] AND SIDE [B] VIEWS OF A MYXOBOLUS SPORE.

(For further explanation see following pages.)

The spore of Myxosporidia is covered by a shell, which is composed of two valves usually symmetrical in form and size that come in contact in the sutural plane. The sutural line is straight in most cases, tho sometimes curved like an S. It is more or less thickened, forming the sutural ridge. The sutural ridge is to be made out clearly in fresh as well as in stained preparations and furnishes important data in regard to the classification of the parasite. The thickness of the shell-valve is usually uniform; in some species (*Myxobolus*), however, it may differ slightly in different parts of the shell. Besides, in many species of *Myxobolus*, the shell differentiates a small triangular intercapsular appendix on the inside at the anterior end directed posteriad between two polar capsules.

The form of the spore varies greatly owing to the shape of the shell together with its variously developed appendages; 1) lateral appendages as in *Ceratomyxa*, 2) anterior processes as in *Myxoproteus*, 3) posterior processes as in *Wardia* (fringe-like), *Mitraspora* (filiform), *Hoferellus* (spinous), *Henneguya* (tail-form), etc.

The surface of the shell may be smooth or exhibit various markings. More or less conspicuous ridges varying in form and number in different species, may run parallel to the sutural line, may show a network-like structure or may exhibit short tooth-like processes arising from the sutural ridge and radiating toward the center of each valve. When the ridges are fine, they form delicate striations, arranged usually parallel to the sutural line. Tho these markings are usually easily seen in vivo, they are very often more readily studied in stained preparations.

Inside of the shell are present the polar capsules and sporoplasm. Gurley (1894:120) and Davis (1917:210) used the term "capsules" instead of polar capsules because of the facts that "the situation implied by the the latter (polar capsule) is not constant" (Gurley) and that "they are often not in the position indicated by the term polar capsule" (Davis). The present writer, however, does not agree with these authors and retains the commonly used term, polar capsule, thruout the present paper on the basis of the fact that these polar capsules are situated at or near the more or less attenuated anterior end in the great majority of species or at each end (in Myxidiidae) of the spore, except in the few cases as in *Wardia* in which they are situated in the central portion and have the foramina at the anterior end of the spore.

The polar capsules may be pyriform or spherical. They are located at or near one end (anterior end) of the spore. In Myxidiidae, one polar capsule is situated at each end, in which case no distinction can be made between the anterior and posterior ends. The end or side opposite to the anterior, is the posterior end of the spore. The number of polar capsules in a spore varies according to the different genera. There is only one polar capsule in the spore of unicapsular *Myxobolus*, four in *Chloromyxum*, two in all the other genera. They may be equal or unequal in form and size. When two polar capsules are located at the anterior end, they may be convergent or divergent. Each has a foramen to the outside of the spore thru the shell in or near the sutural line, thru which the polar filament is extruded. The foramen is observable in the fresh condition. Staining will very often show clearly the canals thru the shell. Each polar capsule has an independent foramen.

In the polar capsule exists a coiled polar filament, which in most cases can be recognized without difficulty in the fresh condition. The polar filament is as a rule a more or less extended, probably hollow thread connected with the polar capsule, which is extruded from the spore thru the foramen under the action of the stimulants such as the digestive fluid of the host or certain chemicals. In *Sphaeromyxa* it is rather short and thick, tapering to a point. The polar filament is coiled around the longest axis of the polar capsule, except in *Sphaeromyxa* in which it is coiled around an axis perpendicular to the longest axis of the polar capsule.

The sporoplasm occupies the extracapsular cavity at the posterior region of the spore. It is of granular structure with almost always two nuclei. Besides, it has an iodophilous vacuole mostly round or oval in the spores of the family Myxobolidae. It occurs thruout the spore stage and is the important character of the said family. The contents of the vacuole is probably of glycogenous nature and is stained deeply with iodine. Small refringent fat globules have also been observed in the spore.

Davis (1917:212) proposed to use capsular and postcapsular sides in place of anterior and posterior ends which have most frequently been used and are also used in the present paper. The latter terms can be employed as properly as Davis' terms except in the case of the Myxidiidae, where both terms, strictly speaking, are inapplicable.

The various abnormal spores are very often encountered in several species, the majority of the spores are of typical form, structure and size. In *Myxosoma* and *Myxobolus*, the spore sometimes develops a short posterior process, which is highly developed in the spore of the genus *Henneguya*.

Young spores, generally speaking, are more rounded in form than the mature form, while the mature spores, as a rule, are of definite form, structure and size characteristic to the species. It should, however, be kept in mind that there is a certain amount of variation among these characters.

As is generally recognized, one must mention whether the spores were measured in fresh condition or in fixed and stained state. The fresh spore is generally more or less larger than the mounted one.

## DEFINITION OF TERMS USED FOR DESCRIPTIONS

*Anterior end.*—The end of the spore where the polar capsules open; in most cases the polar capsules are situated at this end.

*Anterior process.*—The spinous process of the shell at the anterior end of the spore of the genus *Myxoproteus*.

*Breadth.*—The larger diameter of the spore measured at right angles to the length or sutural diameter; the shorter diameter thus measured being the thickness.

*Capsulogenous cell.*—A small island of protoplasm with a nucleus, in which polar capsule becomes differentiated.

*Cyst.*—The vegetative form of more or less conspicuous size in tissues of the host, surrounded usually by a membranous structure composed of the host issue.

*Disporous.*—The character of a trophozoite of forming only two spores.

*Foramen.*—Opening of the polar capsule thru which the polar filament is extruded.

*Front view.*—The view in which length and breadth of the spore are laid horizontally.

*Gemmules.*—A small mass of trophozoite separated from the mother body by plasmotomy. Used by Davis (1917). (See page 105.)

*Iodinophilous vacuole.*—The vacuole in the sporoplasm of the spore of the family *Myxobolidae*, the contents of which are stained brownish with iodine.

*Lateral process.*—The lateral prolongation of the shell-valve at right angles to the sutural plane.

*Length.*—Antero-posterior diameter of the spore in the sutural plane; equivalent to sutural diameter.

*Longitudinal striations.*—Fine ridges or thickenings marked longitudinally on the shell of the spore.

*Mesoplasm.*—An intermediate layer between ectoplasm and endoplasm, coined by Cohn in the case of *Myxidium lieberkühni* (see page 107).

*Mictosporous.*—The character of the trophozoite of forming a variable number of spores in an individual.

*Monosporous.*—The character of the trophozoite of forming a single spore.

*Pansporoblast.*—Coined by Gurley (1893:408) used here in the same meaning, an enclosed area in the endoplasm of the vegetative form, in which two sporoblasts become differentiated.

*Plasmogamy.* Fusion of two trophozoites, coined by Doflein (1898).

*Plasmotomy.*—Division of trophozoite into daughter individuals, coined by Doflein (1898).

*Polar capsule.*—The pyriform or spherical, hollow body in the spore which forms a polar filament.

*Polar filament.*—The filament which is coiled inside the polar capsule.

*Polysporous.*—The character of the trophozoite of forming spores, more than two.

*Posterior filament.*—Fine posterior appendage of the spore.

*Posterior processes.*—Posterior differentiations of the shell.

*Ridge.*—Linear or network-like elevation of the shell of the spore.

*Shell.*—The envelope of the spore.

*Shell-valves.*—Two valves which compose the shell of the spore.

*Sporoplasm.*—The protoplasmic mass found inside of the spore (amebula or sporozoite), usually situated in the posterior portion of the spore.

*Sutural diameter.*—Same as length.

*Sutural edge.*—The edge of the shell-valves cut by the sutural plane.

*Sutural line.*—The line on the shell of the spore marked by the sutural plane.

*Sutural plane.*—The plane on which two shell-valves meet together.

*Sutural ridge.*—The ridge marking the sutural line.

*Tail.*—The posterior prolongation of the valves from the median posterior end; it may be a single process or bifurcated.

*Thickness.*—See breadth.

*Trophozoite.*—The vegetative or multiplicative stage of a Myxosporidian.

*Vegetative form.*—Same as trophozoite.

## CLASSIFICATION OF MYXOSPORIDIA

The classification of Myxosporidia, was first carried out by Thélohan as early as 1892, who considered rightly that the spore was the only reliable means for the purpose. In 1899 and 1901, Doflein introduced into the classification two Legions, Disporea and Polysporea, and a new family. This plan has generally been followed by various authors in dealing with these protozoa.\*

The classification of the said author, however, no longer agrees with our present knowledge of the animals. In the first place, as was pointed out by some authors, for instance Davis (1917:217), it is far from being correct to divide the Myxosporidia into two Legions, Disporea and Polysporea, on the basis of the number of spores formed in each vegetative form, since this differs even in one and the same species as was observed by Léger, Auerbach, Awerinzew, Parisi, Georgévitch, Davis, Kudo and others (see Table IV on page 53).

Auerbach who had observed numerous interesting facts in this group, had adopted Doflein's classification in his splendid work (1910) by simply adding two genera, Zschokkella and Lentospora, to the family Myxidiidae. In the following year (1911), he tried a new classification, on the same basis as Doflein did, by introducing two new Legions besides these two already existing, and by discarding all the families. Thus:

I Monosporea	a) Genus	Coccomyxa
II Mictosporea	a) Genus	Zschokkella
	b) Genus	Myxoproteus
	c) Genus	Myxidium
	d) Genus	Sphaeromyxa
	e) Genus	Chloromyxum
	f) Genus	Sphaerospora
III Disporea	a) Genus	Ceratomyxa
	b) Genus	Leptotheca
IV Polysporea	a) Genus	Myxosoma
	b) Genus	Lentospora
	c) Genus	Myxobolus
	d) Genus	Henneguya
	e) Genus	Hoferellus

As will be distinctly seen from Table IV, the classification not only fails to improve Doflein's classification in bringing together the genera, Myxo-

\* Doflein still uses the same classification in his recent work (1916).

proteus, Myxidium and Sphaeromyxa into Mictosporaea, and Lentospora and Henneguya into Polysporaea, but increases the confusion concerning relationship among the genera.

TABLE IV

Genus	Mono- and di- sporous	Mono- and poly- sporous	Di- sporous	Mono, di- and poly- sporous	Di- and poly- sporous	Poly- sporous	Unknown
<i>Leptotheca</i> 15 species	.		8				7
<i>Ceratomyxa</i> 35 species	3		23		4		5
<i>Myxoproteus</i> 3 species		.	2			.	1
<i>Wardia*</i> 2 species						1	1
<i>Mitraspora*</i> 3 species					2	1	
<i>Chloromyxum</i> 22 species	1	2		2	6	4	7
<i>Sphaerospora</i> 10 species	1		2	1	2	2	2
<i>Sinuolinea*</i> 5 species			2		2	1	
<i>Myxidium</i> 26 species	1		2	2	2	9	10
<i>Sphaeromyxa</i> 7 species						5	2
<i>Zschokkella</i> 4 species	1			1		1	1
<i>Myxosoma</i> 3 species						3	
<i>Lentospora</i> 6 species			2			2	2
<i>Myxobolus</i> 63 species						54	9
<i>Henneguya</i> 32 species				1	1	25	5
<i>Hoferellus</i> 1 species	.	.	..		.	1	

\* These three genera are unknown to Auerbach, except two species which were formerly placed in *Leptotheca* and *Sphaerospora*.



Parisi (1912) followed Auerbach in his paper dealing with Myxosporidia from Italian waters. Poche (1913) put Auerbach's classification in better form as follows:

Order: Myxosporidia

2 Superfamily Mictosporaea

2 Family Myxidiidae

2 Genus Zschokkella

3 Genus Myxoproteus

4 Genus Myxidium

5 Genus Sphaeromyxa

6 Genus Sphaerospora

3 Family Chloromyxidae

7 Genus Chloromyxum

3 Superfamily Disporea

4 Family Ceratomyxidae

8 Genus Ceratomyxa

9 Genus Leptotheca

4 Superfamily Polysporea

5 Family Myxosomatidae (Poche)

10 Genus Myxosoma

11 Genus Lentospora

6 Family Myxobolidae

12 Genus Myxobolus

13 Genus Henneguya

14 Genus Hoferellus

For the same reason given in discussing Auerbach, this, however, is not conformable with the present state of knowledge regarding these protozoa.

It was not until 1917 that the classification of the Myxosporidia approached to a more natural state in the valuable work by Davis (1917: 219-221). He pointed out sharply the unsatisfactory features in Doflein's classification and proposed a different system as follows:

Order: Myxosporidia.

Suborder I Myxosporaea Davis

Family 1 Ceratomyxidae

Genus 1 Leptotheca

Genus 2 Ceratomyxa

Family 2 Sphaerosporidae Davis

Genus 1 Myxoproteus

Genus 2 Sphaerospora

Genus 3 Sinuolinea

Family 3 Myxidiidae

Genus 1 Myxidium

Genus 2 Sphaeromyxa

Genus 3 Zschokkella

Family 4 Chloromyxidae

Genus 1 Chloromyxum

## Suborder II Cystosporea Davis

## Family 1 Myxosomidae\* Davis

Genus 1 Myxosoma

Genus 2 Lentospora

## Family 2 Myxobolidae

Genus 1 Myxobolus

Genus 2 Henneguya

Genus 3 Hoferellus

Thus, Davis selected the form of the spore for the establishment of two suborders and further rearranged the genera into closer positions to show relationship to each other better than any one of the previous authors. He, however, named the suborders according to a secondary character, i.e., the seat of the parasites in the host. According to his definition the trophozoites of the species belonging to Myxosporea are "with few exceptions free living in the body-cavity," while those of Cystosporea "with few exceptions" are tissue parasites.

From TABLE III on page 45, are taken the following data regarding this point:

	Total number of species known	Number of species found in body cavity	Number of species found in tissue	Number of species found in both places	Seat unknown
Myxosporea.....	132	114	14	2	2
Cystosporea.....	105	7	95	1	2

Thus it appears that the terms Myxosporea and Cystosporea do not seem to be properly used. These may be replaced by terms that denote the first and common character of the suborders.

The suggestions as to the adoption of other characters than the spore for the divisions of Myxosporidia, proposed by Awerinzew (1907:831; 1908:64), Auerbach (1910:161) and Davis (1917:217) can only be applied in the future. At the present time, the characters concerning the vegetative form do not appear to afford a better and more natural basis for the classification of Myxosporidia than those of the spore. Thus from the taxonomic point of view the present situation does not seem to be much improved as compared with that at the end of the last century.

The writer proposes in the following pages a new classification based on the characters of the spore.

\* Davis did not notice the establishment of the family Myxosomatidae by F. Poche (1913), including exactly the same genera. See page 54.

## Order MYXOSPORIDIA Bütschli 1881

## Suborder EURYSPOREA nom. nov.

Largest diameter of the spore at right angles to the sutural plane. One polar capsule on each side of the plane. Sporoplasm with no iodophilous vacuole. Vegetative form found in body cavity (except 2 species). Great majority parasites of marine fish. Monosporous, disporous and polysporous.

## Family CERATOMYXIDAE Doflein 1899

With the characters of the suborder.

## Genus LEPTOTHECA Thélohan 1895

Shell-valves of spore hemispherical or shortly rounded. 15 species. Disporous (7 unknown). 14 species in body-cavity; 1 in tissue; all in marine fish. Type species: *Leptotheca agilis* Thélohan.

## Genus CERATOMYXA Thélohan 1892

Shell-valves, conical and hollow, attached on the bases; free ends extended, tapering to more or less sharply pointed or rounded ends. Sporoplasm usually does not fill the cavity, but is located asymmetrically in it. 35 species. Disporous (23 species), monosporous and disporous (3 species), disporous and polysporous (4 species) and unknown (5 species). All (except 2 species in urinary bladder) in the gall-bladder of marine fish. Type species: *Ceratomyxa arcuata* Thélohan.

## Genus MYXOPROTEUS Doflein 1898 emend. Davis 1917

Spores roughly pyramidal; with or without distinct processes from the base of the pyramid. 3 species. Disporous (one species unknown). All in urinary bladder of marine fish. Type species: *Myxoproteus ambiguus* (Thélohan) Doflein.

## Genus WARDIA nov. gen.

Spore form of isosceles triangle with two convex sides. Oval in profile. Surface of shell with fine ridges which turn into fringe-like processes at the posterior end. The polar capsules, large and perfectly spherical, situated at the central portion of the spore, opening at the anterior tip. Two species. Polysporous (one species unknown). Tissue parasite (one species) of fresh-water fish and amphibia, both found in Illinois, U. S. A. Type species: *Wardia ovinocua* nov. spec.

## Genus MITRASPORA Fujita 1912 emend. Kudo

Spores spherical or ovoidal. Two polar capsules pyriform, one situated on each side of the sutural plane. Shell longitudinally striated; with or without long and fine filaments projecting posteriorly in a row at right

angles to the sutural plane at the posterior side. 3 species. Disporous and polysporous. All found in kidney of fresh-water fish. Type species: *Mitraspora cyprini* Fujita.

Suborder SPHAEROSPOREA nom. nov.

Spores spherical or subspherical, with two to four polar capsules. Sporoplasm without iodophilous vacuole. Vegetative form found in body-cavity and tissue. Monosporous, disporous and polysporous. Parasites of marine and fresh-water fish and amphibia.

Family CHLOROMYXIDAE Thélohan 1892\*

Spores with four polar capsules. Monosporous, disporous and polysporous.

Genus CHLOROMYXUM Mingazzini 1890

With the characters of the family. 22 species. 18 in body cavity; 4 in tissue. 7 from marine and 12 from fresh-water fish, 2 in amphibia, 1 in insect. Type species: *Chloromyxum leydigi* Mingazzini.

Family SPHAEROSPORIDAE Davis 1917

Spores with two polar capsules. Monosporous, disporous and polysporous.

Genus SPHAEROSPORA Thélohan 1892

Spores with two polar capsules. Monosporous, disporous and polysporous. 10 species. Body-cavity and tissue. 5 from fresh-water and 5 marine fish. Type species: *Sphaerospora divergens* Thélohan.

Genus SINUOLINEA Davis 1917

Spores with or without lateral processes. Two polar capsules spherical. Sutural line sinuous. 5 species. Disporous and polysporous. In the urinary bladder of marine fish. Type species: *Sinuolinea dimorpha* Davis.

Suborder PLATYSPOREA nom. nov.

Sutural plane of the spore coincides with or at an acute angle to the longest diameter. One or two polar capsules. Sporoplasm with or without an iodophilous vacuole.

Family MYXIDIIDAE Thélohan 1892

Two polar capsules, one at each end. Sporoplasm without any iodophilous vacuole. Spores fusiform.

\* Thélohan (1892) used the terms: Chloromyxidées, Myxididées, Myxobolidées, which Gurley (1893) made over into Chloromyxidae, Myxidiidae, Myxobolidae, so that the credit of recognizing and establishing these families belongs to Thélohan.

## Genus MYXIDIUM Bütschli 1882

Spores more or less regularly fusiform, with pointed or rounded ends. Polar filaments long and fine. 26 species. Monosporous, disporous and polysporous. 22 in body-cavity; 4 in tissue. 15 in marine and 6 in fresh-water fish, 2 in fishes from both waters and 3 in reptilia. Type species: *Myxidium lieberkühni* Bütschli.

## Genus SPHAEROMYXA Thélohan 1892

Spores fusiform, with truncated ends. Polar filament short and thick. Trophozoites large and disc shaped. 7 species. Polysporous (2 unknown). 6 in body-cavity; 1 unknown. 6 in marine fish; 1 in amphibia. Type species: *Sphaeromyxa balbianii* Thélohan.

## Genus ZSCHOKKELLA Auerbach 1910

Spores, semicircular in front view; pointed at ends. Polar capsules large and spherical, opening on the flat edge near the tips. Sutural line usually curved in S-form. 4 species. Monosporous, disporous and polysporous. Body-cavity. 2 from marine and 2 from fresh-water fish. Type species: *Zschokkella hildae* Auerbach.

## Family MYXOSOMATIDAE Poche 1913

Two polar capsules at the anterior end. Sporoplasm without iodophilous vacuole.

## Genus MYXOSOMA Thélohan 1892

Spores ovoidal, flattened and more or less elongated. 3 species. Polysporous. Tissue parasites. 2 in fresh-water and 1 in marine fish. Type species: *Myxosoma dujardini* Thélohan.

## Genus LENTOSPORA Plehn 1905

Spores similar to Myxobolus in form. Sporoplasm without any iodophilous vacuole. 6 species. Disporous and polysporous (2 unknown). 1 in marine and 3 in fresh-water fish, 2 from fishes in both waters. Type species: *Lentospora cerebralis* (Hofer) Plehn.

## Family MYXOBOLIDAE Thélohan 1892

Spores with one or two polar capsules at the anterior end, with or without posterior processes. Sporoplasm with an iodophilous vacuole. Majority polysporous in fresh-water fishes.

## Genus MYXOBOLUS Bütschli 1882

Spores ovoidal or ellipsoidal; flattened. One or two polar capsules at the anterior end. Shell without posterior process. 63 species. Polysporous (9 species unknown). 59 species in tissue; 4 unknown. 5 in marine and 56 in fresh-water fish, 1 in annelid and 1 in amphibia. Type species: *Myxobolus mülleri* Bütschli.

## Genus HENNEGUYA Thélohan 1892

Spores more or less globular or ovoidal. Two polar capsules at the anterior end. Posterior end of the shell-valves prolonged into more or less extended processes, which unite and form a tail in the median line. 32 species. Polysporous, disporous and monosporous. 28 species in tissue and 4 in body-cavity. In fresh-water fish, except one. Type species: *Henneguya psorospermica* Thélohan.

## Genus HOFERELLUS Berg 1898

Spores pyramidal, with two posterior processes from the lateral faces. 1 species. Polysporous. Tissue and body-cavity of fresh-water fish. Type and only species: *Hoferellus cyprini* Doflein.

## DESCRIPTIONS OF GENERA AND SPECIES

### Suborder EURYSPOREA nom. nov.

The definition of the suborder is recorded on page 56.

### Family CERATOMYXIDAE Doflein

1899	<i>Ceratomyxidea</i>	Doflein	1899 : 378
1901	<i>Ceratomyxidae</i>	Doflein	1901 : 182

The characters of the family are described on page 56.

### Genus LEPTOTHECA Thélohan

1895	<i>Leptotheca</i>	Thélohan	1895 : 331
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The characters of the genus are described on page 56.

Type species: *Leptotheca agilis* Thélohan.

### LEPTOTHECA AGILIS Thélohan

[Figs. 1 to 5]

1892	<i>Ceratomyxa agilis</i>	Thélohan	1892 : 962
1895	<i>Leptotheca agilis</i>	Thélohan	1895 : 332
1898	<i>Leptotheca agilis</i>	Doflein	1898 : 294, 297

Habitat: Gall-bladder of *Trygon pastinaca* L. and *Scorpaena* sp.; France, Rovigno, Napoli.

Vegetative form: Form generally elongated. Anterior end rounded where a mass of fat globules is found, while the posterior end terminates in a point. Size not exceeding  $85\mu$  by 20 to  $25\mu$ . The posterior part is sometimes divided into a certain number of lobes. In the protoplasm, the globules are clearly seen. Pseudopodia are localized at the anterior portion of the body. They are long, 40 to  $50\mu$  in length, filiform and very active in moving from back toward front, just like the motion of oars. Disporous.

Spore: Slightly elongated. Dimensions: sutural diameter 6 to  $7\mu$ , breadth 11 to  $12\mu$ .

### LEPTOTHECA ELONGATA Thélohan

[Fig. 6]

1895	<i>Leptotheca elongata</i>	Thélohan	1895 : 332
1898	<i>Leptotheca elongata</i>	Doflein	1898 : 312
1917	<i>Leptotheca elongata</i>	Georgévitch	1917b : 99-106

Habitat: Gallbladder of *Merluccius merluccius* L. (*M. vulgaris*) and *Motella tricirrata*; Marseille, Banyuls, Le Croisic, Napoli, Monaco.

**Vegetative form:** Form variable. Many individuals show, however, a very characteristic form. It is elongated and has the length of about  $120\mu$ . The anterior end is enlarged into a disc-shaped depression, on the edge of which, the branched pseudopodia are formed. The body gradually narrows itself toward the posterior end. Also club-shaped, etc. The short lobose pseudopodia show no movement like that of oars.

**Georgévitch's form:** Young forms, oval or rounded, are attached to the epithelial cells of the bladder with a long filiform pseudopodium at the free end. Such forms often agglomerate in great number.

**Spore:** Form similar to the spore of *Leptotheca agilis*. Dimensions on the average: Sutural diameter 12 to  $15\mu$ , breadth 18 to  $20\mu$ .

#### LEPTOTHECA POLYMORPHA (Thélohan) Labbé

1895	<i>Leptotheca elongata</i>	Thélohan	1895 : 332-333
1899	<i>Leptotheca polymorpha</i>	Labbé	1899 : 88

**Habitat:** Gall-bladder of *Phycis mediterraneus* (*P. phycis* L.); Banyuls.

**Vegetative form:** Form extremely polymorphous, with three main types. 1) Somewhat regularly club-shaped, with lobose pseudopodia, sometimes filiform at one end. 2) Irregular as is the case with *Ceratomyxa truncata*, with long ( $25\mu$ ) ectoplasmic processes, which are motionless or very slow in motion. Lobose pseudopodia are formed actively. 3) More or less rounded with bristle-like filose pseudopodia. Intermediary forms are also found. Often many individuals unite together. The protoplasm is much different from other forms, i.e., more homogeneous and compact. Granules are hardly visible on account of vacuolar appearance.

**Spore:** Dimensions: sutural diameter 10 to  $12\mu$ , breadth 18 to  $20\mu$ , length of polar filament  $40\mu$ .

#### LEPTOTHECA PARVA Thélohan

[Fig. 7]

1895	<i>Leptotheca parva</i>	Thélohan	1895 : 333
1912	<i>Leptotheca parva</i>	Auerbach	1912 : 42-43

**Habitat:** Gall-bladder of *Scomber scombrus* L.; Marseille, Le Croisic, Le Vivier-sur-mer, Kristiansund, Stavanger, Bergen.

**Vegetative form:** Form ordinarily rounded, spherical or subspherical. Often club-shaped. Size not larger than 12 to  $15\mu$  in diameter. Protoplasm finely granular. Pseudopodia lobose.

**Spore:** Small, more or less elongated, curved in arch-form. Dimensions: sutural diameter 3 to  $4\mu$ , breadth 8 to  $10\mu$ .

#### LEPTOTHECA RENICOLA Thélohan

1895	<i>Leptotheca renicola</i>	Thélohan	1895 : 333
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**Habitat:** Urinary tubules of the kidney of *Scomber scombrus* L.; Marseille, Le Croisic.



Vegetative form: Small. No marked character.

Spore: Globular. Form similar to the spore of *Sphaerospora*. Dimensions: sutural diameter  $8\mu$ , breadth  $10\mu$ .

#### LEPTOTHECA HEPSETI Thélohan

1895	<i>Leptotheca hepseti</i>	Thélohan	1895 : 334
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Habitat: Gall-bladder of *Atherina hepsetus* L.; Marseille. Of rare occurrence; Thélohan observed it but once.

Vegetative form: Not described.

Spore: Form triangular with rounded angles. Dimensions: sutural diameter 7 to  $8\mu$ , breadth 12 to  $15\mu$ .

#### LEPTOTHECA PERLATA (Gurley) Labbé

[Fig. 8]

1883		Balbani 1883 : 201, 204
1894	<i>Chloromyxum (Sphaerospora) perlatum</i>	Gurley 1894 : 272
1899	<i>Leptotheca perlata</i>	Labbé 1899 : 88

Habitat: *Acerina cernua* L.; France (?).

Vegetative form: Not described.

Spore: Elliptic. Two small polar capsules converging. Dimensions not given.

#### LEPTOTHECA sp. Awerinzew

[Figs. 16, 17]

1908	<i>Leptotheca</i> sp.	Awerinzew	1908 : 51, 52
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Habitat: Gall-bladder of *Sebastes norvegicus*; Eastern Finmark?

Vegetative form: Rounded form with clear differentiation of protoplasm into ectoplasm and endoplasm. Plasmotomy occurs.

Spore: Undescribed. No figure.

#### LEPTOTHECA MACROSPORA Auerbach

[Fig. 9]

1909	<i>Leptotheca macrospora</i>	Auerbach	1909 : 70-71
1910	<i>Leptotheca macrospora</i>	Auerbach	1910b : 768-769
1910	<i>Leptotheca macrospora</i>	Auerbach	1910c : 167
1912	<i>Leptotheca macrospora</i>	Auerbach	1912 : 42-43

Habitat: Gall-bladder of *Sebastes viviparus* H. Kr. and *S. dactylopterus*; Bergen, Kristiansund (May, September).

Vegetative form: Trophozoites spherical with the average diameter of 26 to  $30\mu$ . Homogeneous ectoplasm layer exhibits somewhat active ameboid movements. Endoplasm, granular in living specimen, is rather sharply distinguishable from the ectoplasm and contains large nuclei.

Spore: Size large. Form resembles to that of *Leptotheca parva*. Dimensions: sutural diameter and thickness  $13\mu$ , breadth  $26\mu$ . Polar capsules short oval, with a length of  $5.2\mu$ , length of polar filament about  $130\mu$  (KOH). In the second host, a few normal and numerous abnormal spores with three or four polar capsules were observed.

#### LEPTOTHECA INFORMIS Auerbach

[Fig. 10]

1910	<i>Leptotheca informis</i>	Auerbach	1910b : 770-771
1912	<i>Leptotheca informis</i>	Auerbach	1912 : 42-44

Habitat: Gall-bladder of *Molva vulgaris* Flem. and *Gadus merlangus*; Bergen, Tjomo.

Vegetative form: Young trophozoites with somewhat long and narrow pseudopodia formed of hyaline ectoplasm; movements active. The protoplasm is differentiated into ectoplasm and endoplasm. When stained, two large ( $7$  to  $9\mu$ ) and two small ( $3$  to  $4\mu$ ) nuclei were observed in an individual,  $27\mu$  long excluding the pseudopodia. Sporulating trophozoites are generally round and each forms two spores, which are developed independently to each other (i.e., not in ordinary pansporoblast). Auerbach observed centrosomes in the nuclei of larger type in division. Disporous.

Spore: Large and heavily built. Greatly curved. Sutural line fairly well marked. Polar capsules round. Dimensions: sutural diameter  $10\mu$ , breadth  $18$  to  $20\mu$ , thickness  $9\mu$ , diameter of polar capsules  $3$  to  $4\mu$ . Sporoplasm contains two nuclei,  $3.5$  to  $4\mu$  in diameter.

#### LEPTOTHECA LONGIPES Auerbach

[Fig. 11]

1910	<i>Leptotheca longipes</i>	Auerbach	1910b : 771
1912	<i>Leptotheca longipes</i>	Auerbach	1912 : 42-43

Habitat: Gall-bladder of *Brosmius brosme* Asc.; Bergen (May).

Vegetative form: Trophozoites elongated or rounded. Only few pseudopodia which are very long. Small forms with a very long process, were observed in large numbers; length of the body being  $10\mu$ , while the process was  $60\mu$  long. Endoplasm contains nuclei of various sizes. Disporous.

Spore: Form similar to that of *Leptotheca informis*, though smaller. Dimensions: sutural diameter  $8$  to  $9\mu$ , breadth  $12$  to  $14\mu$ , thickness  $8\mu$ , diameter of polar capsule  $2.5\mu$ .

#### LEPTOTHECA FUSIFORMIS Davis

[Fig. 12]

1917	<i>Leptotheca fusiformis</i>	Davis	1917 : 222
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Habitat: Gall-bladder of *Cestracion zygæna*; Beaufort (July).

**Vegetative form:** Pyriform, tapering gradually toward the posterior end, which usually terminates in a long, slender process; colorless and transparent. Progressive movements rapid. Endoplasm granular, the granules being more abundant at the anterior end. The average size of full-grown individuals:  $50\mu$  by  $13\mu$ . Disporous.

**Spore:** Elliptical in front view; fusiform in side view. Sutural plane slightly oblique to the longest diameter, the line forming a marked ridge. Polar capsules open on opposite sides of the spore. Sporoplasm finely granular, confined to the central part of spore. Dimensions: sutural diameter  $9\mu$ , breadth  $16\mu$ , polar capsule  $4.5\mu$  long, length of polar filament  $30\mu$ .

### LEPTOTHECA SCISSURA Davis

[Fig. 13]

1917    *Leptotheca scissura*

Davis

1917 : 222

**Habitat:** Gall-bladder of *Dasybatis hastatus* and *Pteroplatea maclura* Le Sue; Beaufort (July, August).

**Vegetative form:** Young form elongated, with long attenuated posterior process; usually slightly constricted just posterior to rounded anterior end, which bears numerous long, filiform pseudopodia. Progressive movement rapid. Ectoplasm distinguishable at the anterior end. Endoplasm usually filled with small, clear, colorless spherules, which become larger and yellowish as the body increases in size. Each spherule contains one to several dark-brown granules, which increase in size and number and finally collect in an irregular clump at the centre of spherule. The larger individuals are usually flattened dorso-ventrally. The posterior end is divided into long slender processes, presenting sometimes a network caused by the fusion of two or more adjacent processes. Full-grown forms: length  $125$  to  $150\mu$ , breadth  $20$  to  $25\mu$ . The longest observed,  $195\mu$  by  $16\mu$ . Disporous.

**Spore:** Elliptical in front view; somewhat flattened along the posterior side. Sutural line distinct and at right angles to the longest diameter. Polar capsules have foramina at some distance from the capsular margin. Sporoplasm finely granular, nearly filling both valves. Dimensions: sutural diameter  $11\mu$ , breadth  $22\mu$ , diameter of polar capsule  $4\mu$ .

### LEPTOTHECA LOBOSA Davis

[Fig. 14]

1917    *Leptotheca lobosa*

Davis

1917 : 223

**Habitat:** Urinary bladder of *Paralichthys dentatus* L.; Beaufort (July).

**Vegetative form:** Usually spherical which may form a large rounded pseudopodium composed of ectoplasm. Body colorless and transparent to translucent. Ameboid movements very slow. Ectoplasm contains coarse granules, which are of uniform size and very distinct. Endoplasm

less granular and more transparent than ectoplasm, containing numerous large, yellow, fat globules, which are abundant in large forms. Diameter up to  $24\mu$ . Disporous.

Spore: Elliptical in front view; valves slightly tapering but rarely alike. Sutural line forming a sinuous ridge. Polar capsules open at some distance from the anterior margin. Sporoplasm nearly filling both valves. Free spores are often seen to remain united at the sutural line. Dimensions: sutural diameter 9 to  $10\mu$ , breadth 16 to  $18\mu$ ; diameter of polar capsule  $3\mu$ .

### LEPTOTHECA GLOMEROSA Davis

[Fig. 15]

1917	<i>Leptotheca glomerosa</i>	Davis	1917 : 223
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Habitat: Urinary bladder of *Paralichthys albiguttus*; Beaufort.

Vegetative form: Rounded or somewhat irregular in shape, with short lobose pseudopodia. Body transparent and colorless. Ameboid movements slow. Ectoplasm hyaline, forming a distinct outer layer. Endoplasm finely granular, with numerous small fat globules varying in size. Almost entire body is used for spore formation. Diameter of rounded sporulating trophozoite about  $11\mu$ . Disporous.

Spore: Approximately cylindrical; valves rounded at ends. The coiled polar filament not visible in the polar capsule. Sutural line at right angles to the longest diameter. Sporoplasm finely granular, fills the extracapsular cavity of spore. Dimensions: sutural diameter  $4.5\mu$ , breadth  $9\mu$ , diameter of polar capsule  $2\mu$ .

### Genus CERATOMYXA Thélohan

1892	<i>Ceratomyxa</i>	Thélohan	1892 : 169, 171, 175
1895	<i>Ceratomyxa</i>	Thélohan	1895 : 334

The characters of the genus described on page 56.

Type species: *Ceratomyxa arcuata* Thélohan.

### CERATOMYXA ARCUATA Thélohan

[Figs. 18 to 22]

1892	<i>Ceratomyxa arcuata</i>	Thélohan	1892a : 1091
1895	<i>Ceratomyxa arcuata</i>	Thélohan	1895 : 335-336
1899	<i>Ceratomyxa arcuata</i>	Labbé	1899 : 90
1912	<i>Ceratomyxa arcuata</i>	Parisi	1912 : 290-291
1913	<i>Ceratomyxa arcuata</i>	Jameson	1913 : 2
1916	<i>Ceratomyxa arcuata</i>	Georgévitch	1916a : 3

Habitat: Gall-bladder of *Pagellus centrodontus* C. et V., *Crenilabrus melops* L., *Motella tricirrata* Bl., *Ophidium vasalli*, *Gobius paganellus* L., *Heliases chromis* Gthr.; *Scorpaena scrofa* L., *S. porcus* L.; France (Marseille, Banyuls, Concarneau, Roscoff), Italy (Napoli, summer), Monaco (May).

**Vegetative form:** Polymorphous; generally club-shape, pseudopodia localized at the broad end; the other end cylindrical or terminating in a sharp point. Some other different forms. Pseudopodia, always localized, lobose pointed at the extremities. Ectoplasm hyaline and thin. Endoplasm contains fat globules and particular elements, mostly large refractive globules, which seem to disappear in the sporulating individuals. Dimensions (maximum): length 35 to 40 $\mu$ , breadth 12 to 15 $\mu$ , pseudopodia about 10 $\mu$  long. Disporous.

**Spore:** Arch form. Shell valves equal. Sporoplasm occupies the extracapsular cavity of the spore. The length varies rather considerably according to the development of the lateral processes, which are occasionally acuminate or very short. Often extremities are rounded. Dimensions (Thélohan); breadth 20 to 30 $\mu$ , sutural diameter 5 to 8 $\mu$ . Parisi's measurements: breadth 25 to 31 $\mu$ , sutural diameter 5.5 to 6 $\mu$ , length of polar capsules 3.5 to 4 $\mu$ , length of polar filaments 25 $\mu$ .

**Remarks:** The writer agrees with Parisi in eliminating Labbé's two subspecies (1899:90), as they are too arbitrary.

#### CERATOMYXA SPHAERULOSA Thélohan

[Figs. 23 to 24]

1892	<i>Ceratomyxa sphaerulosa</i>	Thélohan	1892 : 171
1895	<i>Ceratomyxa sphaerulosa</i>	Thélohan	1895 : 334-335
1909	? <i>Ceratomyxa sphaerulosa</i>	Auerbach	1909 : 80
1912	<i>Ceratomyxa sphaerulosa</i>	Auerbach	1912 : 4, 45
1916	<i>Ceratomyxa sphaerulosa</i>	Georgévitch	1916a : 3

**Habitat:** Gall-bladder of *Mustelus canis* Mitch. (*M. vulgaris*), *Galeus galeus* L. (*G. canis*), *Clupea harengus*, *Scullium canicula* Cuv.; St-Valéry-en-Caux, Roscoff, Bergen, Monaco (May).

**Vegetative form:** Form more or less definite among the adults. Generally elongated. Both ends slightly attenuated. Wide in the middle part of the body. Lobose pseudopodia at one of the extremities. Others more massive or more or less regularly spherical, in which case the pseudopodia are formed from the whole surface. Spherical form does not exceed 50 to 60 $\mu$  in diameter. Other forms 90 to 100 $\mu$  by 30 to 40 $\mu$  (largest). Young forms colorless and are more variable than the adults. Protoplasm homogeneous and finely granular. Adult form, on the contrary, yellowish or greenish yellow. The endoplasm is filled with small (5 $\mu$  in diameter) spheres, in the centre of which 5 to 6 small granules, yellowish brown or greenish in color, are present. Disporous.

**Spore:** Remarkably large. Polar filament can be seen *in vivo* (easily extruded by KOH, ether, etc.) Sporoplasm occupies one of the shell-valves, while a small mass of very pale looking substance is seen in the other. Dimensions: sutural diameter 10 to 12 $\mu$ , breadth 90 to 100 $\mu$ , subspherical polar capsule 6 to 7 by 5 $\mu$ , sporoplasm 12 to 15 by 8 to 9 $\mu$ .

## CERATOMYXA PALLIDA Thélohan

1895	<i>Ceratomyxa pallida</i>	Thélohan	1895 : 336-337
1898	<i>Ceratomyxa pallida</i>	Doflein	1898 : 341
1916	<i>Ceratomyxa pallida</i>	Georgévitch	1916b : 2, 3

Habitat: Gall-bladder of *Box boops* L. and *B. salpa* L.; Marseille, Villefranche, Rovigno, Monaco (May).

Vegetative form: Ordinarily spherical not exceeding 16 to 20 $\mu$  in diameter. Many individuals often found in massive groups. Pseudopodia lobose and mostly short. Protoplasm extremely pale with fine granules.

Spore: Dimensions: sutural diameter 5 $\mu$ , breadth 25 to 30 $\mu$ .

## CERATOMYXA GLOBULIFERA Thélohan

[Fig. 25]

1895	<i>Ceratomyxa globulifera</i>	Thélohan	1895 : 338
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Habitat: Gall-bladder of *Merluccius merluccius* L. (*M. vulgaris*); Marseille, Banyuls.

Vegetative form: Polymorphous. Elongated into long branches, including endoplasm. Endoplasm contains small refractive globules.

Spore: Elongated. Shell-valves unequal, one being longer and finer than the other. Dimensions: sutural diameter 10 $\mu$ , breadth 50 $\mu$ .

## CERATOMYXA APPENDICULATA Thélohan

[Fig. 26]

1892	<i>Ceratomyxa appendiculata</i>	Thélohan	1892a : 963-964
1895	<i>Ceratomyxa appendiculata</i>	Thélohan	1895 : 337
1898	<i>Ceratomyxa appendiculata</i>	Doflein	1898 : 300, 311

Habitat: Gall-bladder of *Lophius piscatorius* L., *L. budegassa* Spin.; Roscoff, Le Croisic, Marseille, Banyuls, Napoli, Rovigno.

Vegetative form: Extremely polymorphous. Young form spherical, spatulaform, club-shape, etc. In adult form, the main thick part of the body, in which spore formation takes place, forms 1 to 6 long prolongations, twice or three times longer than the main part of the body. Pseudopodia lobose, filiform or elongated with enlargements. Disporous.

Spore: Lateral prolongations of shell-valves well developed. Dimensions: sutural diameter 5 to 7 $\mu$ , breadth 50 $\mu$ .

## CERATOMYXA TRUNCATA Thélohan

[Fig. 27]

1895	<i>Ceratomyxa truncata</i>	Thélohan	1895 : 336
1912	<i>Ceratomyxa truncata</i>	Parisi	1912 : 289-290

Habitat: Gall-bladder of *Clupea pilchardus* Walb. (*Alosa sardina*); Marseille, Villefranche, Napoli (August, September).

Vegetative form: Polymorphous. Ordinarily more or less rounded, with lobose pseudopodia. Pseudopodia long and often shows very active movements. Endoplasm very finely granular, contains small fat globules which are found in irregular mass or in a circular form. Disporous.

Spore: Valves are short and truncate. Sporoplasm occupies the whole cavity. Spores with three valves are frequently encountered. Dimensions: breadth  $25\mu$ ,  $5\mu$  in sutural diameter. According to Parisi, spores with two shell-valves are rather few (10%), while those with three (70%) and four shell-valves (20%) prevail in number! Dimensions: breadth 20 to  $30\mu$ , length of the polar filament  $45\mu$ .

### CERATOMYXA RETICULARIS Th  lohan

[Fig. 28]

1895    *Ceratomyxa reticularis*    Th  lohan    1895 : 337-338

Habitat: Gall-bladder of *Trachinus draco* L.; Banyuls.

Vegetative form: Extremely polymorphous. Generally spherical or club-shaped. Well developed trophozoites have the similar form as in *C. appendiculata*. Endoplasm highly reticular, with refringent fluid.

Spore: Shell valves are short and truncate, one of which is curved to the rear. Dimensions: sutural diameter 12 to  $15\mu$ , breadth 45 to  $50\mu$ .

### CERATOMYXA INAEQUALIS Doflein

[Fig. 29]

1898    *Ceratomyxa inaequalis*    Doflein    1898 : 284-285

Habitat: Gall-bladder of *Crenilabrus mediterraneus* and *C. pavo*; Napoli.

Vegetative form: Form usually club-shaped. Protoplasm in active motion, is differentiated distinctly into ectoplasm and endoplasm. Body yellowish brown by the presence of granules in endoplasm. Inactive formation of pseudopodia. Ameboid movements or progressive movements by means of the posterior process. Size: 20 to  $40\mu$  by 5 to  $10\mu$  in average. Length of the posterior process up to  $30\mu$ . After spore formation, only two nuclei remain in protoplasm, which apparently degenerate later. Disporous.

Spore: Elliptical, somewhat flattened. Massive. Very transparent. Both ends round, but unequally built, i.e., one end is club-shaped. Polar capsules are somewhat round and are bound to the shell by protoplasmic bridges. The polar filament is not seen in fresh spores. Dimensions: sutural diameter  $6\mu$ , breadth  $31\mu$ , diameter of the polar capsule  $2.5\mu$ , length of polar filament is half breadth of the spore (diluted nitric acid).

## CERATOMYXA LINOSPORA Doflein

[Figs. 30 to 31]

1898 *Ceratomyxa linospora*

Doflein

1898 : 285

Habitat: Gall-bladder of *Labrus turdus*; Napoli.

Vegetative form: Club- or spindleshape. Protoplasm highly granulated. Body whitish grey, though very transparent. Pseudopodia very fine and only formed at the anterior end of the body. Size: 30 to 35 $\mu$  by 16 to 18 $\mu$ . Disporous.

Spore: Form symmetrical with long thread-like lateral processes. In sporoblast, the processes are wound around the spore. It is twice as long as the breadth of the spore. Polar capsules large and spherical pyriform. Dimensions: total breadth 50 $\mu$ , breadth of the main part of the spore 10 to 12 $\mu$ , sutural diameter 5 $\mu$ , length of lateral process 20 $\mu$ . "Polar filament was too fine to be measured."

## CERATOMYXA RAMOSA Awerinzew

[Figs. 32 and 33]

1907 *Ceratomyxa ramosa*

Awerinzew

1907 : 831-834

\*1908 *Ceratomyxa ramosa*

Awerinzew

1908 : 60-66

Habitat: Gall-bladder of *Hippoglossus vulgaris* Flemm.; Kjellebjord, Murman coast.

Vegetative form: Form irregular ameboid, owing to the presence of peculiar pseudopodia. The middle part of the body is enlarged into an ellipsoidal form, where nuclei and sporoblasts are present. From this part two, rarely one or three processes are formed, which branch out several pseudopodia of different length. The finer portions of pseudopodia anastomose each other and form a characteristic and remarkable network. Differentiation of protoplasm is not very distinct. Ectoplasm is not well developed, tho covering the entire surface of the body as a thin layer. Endoplasm slightly vacuolated and granular, forms the greater part of the body. Disporous and polysporous.

Spore: Form and size (?) resemble *C. arcuata*. Slightly curved toward the posterior side. Valves usually unequally built, one being longer than the other. Sporoplasm almost always asymmetrically situated in the shell. Polar capsules on each side of the sutural plane and of the plane perpendicular to the sutural plane, cutting the spore into two equal parts. Young spores in development ellipsoidal to kidney bean shape. Dimensions: sutural diameter 12 to 20 $\mu$ , breadth 50 to 80 $\mu$ .

\*Professor J. Zeitlin has kindly translated some part of the paper, for which the writer expresses his thanks.



## CERATOMYXA DREPANOPSETTAE Awerinzew

[Figs. 34 to 39]

1907	<i>Ceratomyxa</i> sp.	Awerinzew	1907 : 832-833 <sup>4</sup>
1908	<i>Ceratomyxa drepanopsettae</i>	Awerinzew	1908 : 1-41, 45-47
1909	<i>Ceratomyxa drepanopsettae</i>	Awerinzew	1909 : 74-112
1912	<i>Ceratomyxa drepanopsettae</i>	Auerbach	1912 : 44-45
1918	<i>Ceratomyxa drepanopsettae</i>	Kudo	1918 : 14-15

Habitat: Gall-bladder of *Pleuronectes platessa*, *P. flesus*, *Drepanopsetta plattessoides*, *Hippoglossus vulgaris*, *Hippoglossoides limandoides* and *Paralichthys dentatus*; Murmankuste, Kabelvaag, Rorvik, Tjomo, Woods Hole (August, September).

Vegetative form: Polymorphous. Usually very much elongated and slender forms. Protoplasm differentiated. Endoplasm coarsely granular. Pseudopodia lobose and filiform (2 to  $3\mu$ ), with which the trophozoites attach themselves to the epithelium of the bladder. Disporous.

Spore: Curved toward the posterior side. Shell with rounded ends. Valves almost always unequally built. Dimensions: breadth 50 to  $80\mu$ . Auerbach's form: Form variable. Size: sutural diameter about 12 to  $14\mu$ , breadth about  $56\mu$ , diameter of polar capsule about 4 to  $6\mu$ , length of the cavity in which the sporoplasm is located about  $34\mu$ . Kudo's form: Variable. Sutural diameter 8 to  $10\mu$ , average breadth  $64\mu$ , diameter of polar capsule  $6\mu$ .

## CERATOMYXA TYLOSURI Awerinzew

[Figs. 40 and 41]

1913	<i>Ceratomyxa tylosuri</i>	Awerinzew	1913a : 153
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Habitat: Gall-bladder of *Tylosurus schismatorhynchus*; Lorenzo Marques, Delagoa Bay (Africa).

Vegetative form: Large, irregular, disc-like or large ameboid, with blunt lobose pseudopodia and highly granular protoplasm.

Spore: Large. The anterior edge arch-shape, while the posterior edge has two small horns which are located symmetrically to the sutural line. Polar capsules elongated and are separated from binuclear sporoplasm by a special membrane. Rarely spore with three polar capsules. Dimensions breadth 124 to  $140\mu$ , sutural diameter 40 to  $45\mu$ , thickness 25 to  $30\mu$ .

## CERATOMYXA (?) SPARI Awerinzew

[Figs. 42 and 43]

1913	<i>Ceratomyxa</i> (?) <i>spari</i>	Awerinzew	1913a : 153-154
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Habitat: Gall-bladder of *Sparus berda*; Lorenzo Marques, Delagoa Bay (Africa).

**Vegetative form:** Large (100 to 120 $\mu$ ), disc-form ameoboid, containing a large number of enclosures and granules of different size. In one case, a number of this form, carrying no spore, underwent budding, which resulted in forming spherical forms of various size, some of which divided again into 2 to 6 parts (Plasmotomy?). • Monosporous and disporous.

**Spore:** More or less curved. Two polar capsules lie closely together on each side of the sutural plane. Ends of shell-valves are rounded. Dimensions: breadth 50 to 60 $\mu$ , sutural diameter 12 to 15 $\mu$ , thickness 12 to 15 $\mu$ , polar filament very long (length not given).

**Remarks:** Awerinzew thinks this is the intermediate form between *Leptotheca* and *Ceratomyxa*.

#### CERATOMYXA sp. (?) Awerinzew

1913	<i>Ceratomyxa</i> sp. (?)	Awerinzew	1913a : 154
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**Habitat:** Gall-bladder of *Scatophagus argus*; Delagoa Bay (Africa).

**Vegetative form:** Small, disc-form ameoboid (25 to 35 $\mu$ ), containing two spores of indistinct contour, on account of incomplete formation of the shell. Two spores, apparently, developed in one pansporoblast. Disporous.

**Spore:** Form could not exactly be made out. Polar capsules were arranged like those of other *Ceratomyxa*.

#### CERATOMYXA sp. (?) Awerinzew

1913	<i>Ceratomyxa</i> sp. (?)	Awerinzew	1913a : 154-155
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**Habitat:** Gall-bladder of *Rhinobathus* Awer. (?); Lorenço Marques (Africa).

**Vegetative form:** Irregular shape. Endoplasm highly granular. In the epithelial layer of the gall-bladder numerous, spherical cysts (30 to 35 $\mu$ ) were found. Two spores are formed in one pansporoblast. Disporous.

**Spore:** Cylindrical with broad and slightly rounded ends. Dimensions: sutural diameter 16 to 19 $\mu$ , breadth 70 to 80 $\mu$ , thickness 16 to 19 $\mu$ .

#### CERATOMYXA ACADIENSIS Mavor

[Figs. 44 to 47]

1915	<i>Ceratomyxa acadiensis</i>	Mavor	1915 : 27-30
1916	<i>Ceratomyxa acadiensis</i>	Mavor	1916 : 551-574

**Habitat:** Gall-bladder of *Urophycis chuss* (trophozoites are attached to undetermined Myxosporidia, see p. 176), *Zoarces angularis*, *Pseudopleuronectes americanus*; New Brunswick (Canada) (July to September).

**Vegetative form:** Polymorphous. Typically club-shaped with very long tail, or irregularly stellate. Pseudopodia show rigidity. Sometimes

clumps of protoplasm along their length, which are connected by thin hyaline filaments of ectoplasm. Differentiation of protoplasm is usually observable at the anterior region. Dimensions: length, excluding tail, 12 to 15 $\mu$ , breadth 10 to 20 $\mu$ , tail up to 60 $\mu$ . Disporous.

Spore: Wide, short and slightly compressed dorso-ventrally, with very long fine lateral filaments. Polar capsules spherical. Polar filament invisible *in vivo*. Dimensions: breadth 40 to 50 $\mu$ , sutural diameter 7 to 8 $\mu$ , diameter of polar capsule 3 to 4 $\mu$ , length of polar filament 70 $\mu$ , length of lateral filaments 250 to 300 $\mu$ .

### CERATOMYXA sp. Georgévitch

1916	<i>Ceratomyxa</i> sp.	Georgévitch	1916a : 3
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Habitat: Gall-bladder of *Muraena* sp.; Monaco (May).

Vegetative form: No description.

Spore: No description. No figure.

### CERATOMYXA CORIS Georgévitch

[Fig. 48]

1916	<i>Ceratomyxa coris</i>	Georgévitch	1916a : 4-5
1917	<i>Ceratomyxa coris</i>	Georgévitch	1917a : 1-20

Habitat: Gall-bladder of *Coris julius*, *C. giofredi*; Villefranche (March, June).

Vegetative form: Various forms, club-shape, spherical or elongated, with lobose or filiform pseudopodia. Disporous and rarely Polysporous.

Spore: More or less ellipsoidal. Lateral prolongations of the shell-valves short and truncate. Sutural line straight. Sporoplasm, elongate, rounded, elliptical, fills a part of the extracapsular cavity of the spore. Polar capsules rounded, almost spherical, not converging. Dimensions not given.

Remarks: Georgévitch observed (1917: Fig. 30) that spores of *Glugea marionis* occurred in disporous trophozoite of *Ceratomyxa coris*, which he thought to have happened accidentally by plasmogamy of these two Cnidosporidia. The above mentioned figure, however, strongly suggests that *G. marionis* may be leading parasitic life in the trophozoite of *C. coris*.

### CERATOMYXA HEROUARDI Georgévitch

[Fig. 49]

1913	<i>Leptotheca</i> (?) sp.	Jameson	1913 : 2
1916	<i>Ceratomyxa herouardi</i>	Georgévitch	1916a : 5-8
1916	<i>Ceratomyxa herouardi</i>	Georgévitch	1916b : 717-19, 983-985
1917	<i>Ceratomyxa herouardi</i>	Georgévitch	1917 : 375-399

Habitat: Gall-bladder of *Box Salpa* L.; Monaco (May).

**Vegetative form:** Polymorphous. Elongated with same breadth or tapering to one end; club-shaped with roundish enlargements. Young trophozoites spherical or pyriform. Pseudopodia long and narrow or broad and bi- or multi-lobate. Body colorless both in the young and the adult. Protoplasm homogeneous and finely granular. Disporous and polysporous. Spores are found inside of the endoplasm and in the roundish buds, ordinarily two spores being formed in each bud. Number of buds on one trophozoite varies. Plasmotomy by budding and division.

**Spore:** Elongated elliptic. Polar capsules spherical and large. Sutural plane cuts the spore into exactly equal two parts. Two nuclei in sporoplasm are rather small and are always in one of the shell-valves. Dimensions not given.

**Remark:** The form, mentioned by Jameson in the same seat, host and locality, that "has something of the appearance of a *Leptotheca*" and that is also "almost certainly neither of the two *Myxosporidia*—*Ceratomyxa pallida* and *Henneguya neapolitana* . . .," is probably identical with the present form.

#### CERATOMYXA MESOSPORA Davis

[Fig. 50]

1917 *Ceratomyxa mesospora*

Davis

1917 : 223-224

**Habitat:** Gall-bladder of *Cestracion zygaena*, *C. tiburo*; Beaufort (July).

**Vegetative form:** Pyriform, elongate, with long, slender posterior process. Numerous filiform pseudopodia at anterior end. Progressive movements rapid. Body colorless. No sharp demarcation between ectoplasm and endoplasm. Endoplasm finely granular and filled with small, colorless, homogeneous spherules. Spherules absent at anterior end. Size: total length 70 to 85 $\mu$ , length exclusive of posterior process 50 to 75 $\mu$ , breadth 20 to 25 $\mu$ . Disporous.

**Spore:** Greatly elongate, each valve forming a slightly tapering cone, rounded at the apex. Valves not compressed. Sutural plane forming an acute angle with the longest diameter. Polar capsules conspicuous. Coiled polar filaments very distinct. Polar capsules are remarkable in that they are asymmetrically situated, one being always located in the widest part of the spore, while the other being a little to one side. Sporoplasm asymmetrically situated, sometimes being entirely confined to the larger valve. Dimensions: breadth 50 to 65 $\mu$ , sutural diameter about 8 $\mu$ , diameter of polar capsule 4.5 $\mu$ , length of polar filament 90 $\mu$ .

**Remarks:** Similar to *C. sphaerulosa* Thél. and occurs with *C. recurvata* Davis in the same organ.

#### CERATOMYXA SPHAIROPHORA Davis

[Fig. 51]

1917 *Ceratomyxa sphaerophora*

Davis

1917 : 224

**Habitat:** Gall-bladder of *Scoliodon terrae-novae*; Beaufort.

**Vegetative form:** Pyriform, elongate. Numerous fine filiform pseudopodia at anterior end. Progressive movements rapid. Body colorless and transparent. Ectoplasm clear and homogeneous. Structure of endoplasm highly variable, in majority of trophozoites filled with transparent homogeneous spherules. Small fat globules at the anterior end. In some sporulating individuals, the endoplasm shows vacuolated structure without any spherules, usually, however, sporulating trophozoites exhibit well-defined spherules. The spherules or vacuoles, as the case may be, are separated by a thin layer of distinctly granular endoplasm containing numerous rod-shaped or rounded, colorless bodies, which in their appearance are strikingly like small bacteria tho they are not bacteria, as they fail to take Giemsa stain. Size of sporulating trophozoites 100 to 110 $\mu$  by 25 $\mu$ . Disporous.

**Spore:** Shell-valves greatly elongated, tapering gradually toward the ends. Long, attenuated ends of valves hollow and so fragile that it is almost impossible to find an example in which they are not more or less distorted. Sutural plane perpendicular or only slightly oblique to the longest diameter. Polar capsules are spherical and large; slightly convergent, opening some distance apart on the anterior side. Coiled polar filament distinct. Sporoplasm confined to large, central part of spores, but extending farther into one valve than the other. Dimensions: total breadth 115 to 140 $\mu$ , sutural diameter about 12 $\mu$ , diameter of polar capsules 6 $\mu$ , length of polar filament 75 $\mu$ .

### CERATOMYXA TAENIA Davis

[Figs. 52 and 53]

1917    *Ceratomyxa taenia*

Davis

1917 : 224-225

**Habitat:** Gall-bladder of *Scoliodon terrae-novae*; Beaufort.

**Vegetative form:** Similar to those of *C. sphairophora* Davis, and no character has been found by which they may be distinguished. Sporulating trophozoites can be easily distinguished on account of the very different appearance of the spore and their different arrangement within the trophozoites. The spores of this species are situated, as is usually the case in *Ceratomyxa*, with the greater part of the spore parallel to the long axis of the trophozoite, only a part of one valve being bent back along the rest of the spore. Size: sporulating trophozoites length 80 $\mu$ , breadth 25 $\mu$ . Disporous.

**Spore:** Valves greatly elongated. Shell very thin, the membrane on opposite sides of each valve being in contact for about two-thirds of its length, forming a thin ribbonlike structure; basal third of each valve only slightly compressed; terminal ribbonlike portion of each valve usually twisted so that plane of ribbon is at right angles to the main part of the spore. Polar capsules small, pyriform to spherical and convergent. Coiled polar filament indistinct. Sutural plane perpendicular to the longest

diameter. Sporoplasm finely granular, filling the basal third of each valve, sometimes extending farther into one valve than the other. Dimensions: breadth 140 to 150 $\mu$ , breadth of central portion 45 $\mu$ , sutural diameter 6 $\mu$ , diameter of the polar capsules 3 $\mu$ .

### CERATOMYXA ATTENUATA Davis

[Fig. 54]

1917 *Ceratomyxa attenuata*

Davis

1917 : 225

Habitat: Gall-bladder of *Scoliodon terrae-novae*; Beaufort (July).

Vegetative form: Elongate, pyriform, with long, tapering posterior process; at anterior end numerous long filiform pseudopodia. Progressive movements rapid. Ectoplasm distinct only at anterior end. Endoplasm filled with small, refractive, yellowish or brownish granules, which are uniformly distributed throughout the trophozoite. Between the brownish granules, the endoplasm is clear and colorless, not granular, except at extreme anterior end where it contains a clump of small fat globules. Size of full-grown trophozoites 100 to 120 by 27  $\mu$ . Disporous.

Spore: Valves greatly elongated; a symmetrical, one valve being about 15 $\mu$  shorter than the other and ending abruptly; the longer valve tapering gradually to a point. About midway of each valve, is a thin septum; external to the septum the valves are empty. Polar capsules are large, opening on the anterior margin. Coiled polar filaments distinct. Sutural plane oblique to longitudinal axis, usually forming a ridge. Sporoplasm asymmetrically situated in central part of the spore. Dimensions: breadth 115 $\mu$ , sutural diameter 9 $\mu$ , diameter of polar capsules 4.5 $\mu$ , length of polar filament 60 $\mu$ .

### CERATOMYXA RECURVATA Davis

[Figs. 55 and 56]

1917 *Ceratomyxa recurvata*

Davis

1917 : 225-226

Habitat: Gall-bladder of *Cestracion zygaena*; Beaufort (July).

Vegetative form: Pyriform with long, slender posterior process. Body colorless. Actively motile, forming filiform pseudopodia of ectoplasm at anterior end. Endoplasm colorless and granular, filled with large, homogeneous spherules. Full-grown trophozoites 130 to 175 $\mu$ , length of the main body about 100 $\mu$ . Spores are developed singly from distinct sporoplasts and not necessarily in pairs. Disporous and polysporous (up to 10 spores, 6 and 8 are common numbers).

Spore: Valves greatly curved toward the posterior side, usually symmetrical, but occasionally one may be much more incurved than the other. Valves circular in cross section at the base but toward the ends greatly

flattened. Ends of valves sharply pointed. Polar capsules large, opening at some distance from the anterior margin. Coiled polar filaments distinct. Sporoplasm finely granular usually extending farther into one valve than the other. Dimensions: breadth between points of greatest curvature about  $16\mu$ , sutural diameter 8 to  $9\mu$ , diameter of polar capsules  $4.5\mu$ .

### CERATOMYXA LUNATA Davis

[Figs. 57 to 60]

1917 *Ceratomyxa lunata*

Davis

1917 : 226-227

Habitat: Gall-bladder of *Galeocerca tigrinus*; Beaufort (August).

Vegetative form: Pyriform, rounded after being on the slide for some time. Progressive movements slow. Endoplasm filled with large, homogeneous spherules, which are usually colorless, sometimes light yellow. At extreme anterior end, the endoplasm contains numerous small fat globules. Disporous.

Spore: Considerably variable in size and form. The larger and more typical are more or less crescent-shaped; symmetrical; valves curved toward rear, terminating in more or less rounded ends. Polar capsules large and open on opposite sides of spore. Coiled polar filament distinct. Sporoplasm finely granular, symmetrically situated in spore. Smaller spores differ from large ones chiefly in size; valves are much shortened and have a greater curvature, with more distinctly rounded ends. Dimensions: breadth  $30\mu$  (longest  $38\mu$ ), sutural diameter  $9\mu$ , diameter of polar capsules  $4\mu$ , length of polar filament  $37\mu$ . Small forms: breadth  $15\mu$ , sutural diameter  $7\mu$ , diameter of polar capsules  $3\mu$ .

### CERATOMYXA ABBREVIATA Davis

[Fig. 61]

1917 *Ceratomyxa abbreviata*

Davis

1917 : 227

Habitat: Gall-bladder of *Scoliodon terrae-novae*; Beaufort (August).

Vegetative form: Elongate, pyriform, with usually a very long, slender posterior process. Body colorless. Progressive movements rapid. Distinct differentiation of protoplasm, posterior process usually composed of ectoplasm (rarely endoplasm may extend into it for a short distance). Pseudopodia, short, tapering or filiform at anterior end. Dimensions: length up to  $90\mu$ , breadth 10 to  $12\mu$ , diameter of rounded sporulating trophozoites about  $27\mu$ . Disporous.

Spore: Roughly crescent-shaped; sutural diameter exceptionally great in comparison with the breadth. Ends of valves rounded, slightly asymmetrical. Shell exceptionally tough and resistant to reagents. Polar capsules large, prominent and open on opposite sides of spore. Sporoplasm finely granular, confined entirely to one valve. Dimensions: breadth  $17\mu$ , sutural diameter  $14\mu$ , diameter of polar capsules  $4.5\mu$ .

## CERATOMYXA FLAGELLIFERA Davis

[Fig. 62]

1917 *Ceratomyxa flagellifera*

Davis

1917 : 227

Habitat: Gall-bladder of *Carcharhinus* sp?; Beaufort (July).

Vegetative form: Pyriform, short, tapering toward the posterior end, sometimes dividing into a number of long, slender, transparent processes. Extremely long filiform pseudopodia, developed at anterior end, can be seen to sweep slowly back like a whiplash until they come to lie by the side of the body. Progressive movements slow. Ectoplasm clear, transparent, forming a distinct layer at anterior end. Endoplasm in large trophozoites filled with large numbers of rod-shaped, bacteria-like bodies, which are more abundant in the anterior half than in the posterior. Endoplasm in younger trophozoites, with much less or without any bacteria-like bodies, shows a vacuolated structure. Size up to 115 to 120 $\mu$  in length and 40 to 45 $\mu$  in breadth. Disporous.

Spore: Valves greatly elongated, conical, with rounded ends. Sutural ridge well marked. Polar capsules large, opening on opposite sides of spore. Coiled polar filament very distinct. Sporoplasm granular, symmetrically situated, but extending only a short distance into each valve. Dimensions: breadth 118 $\mu$ , sutural diameter 12 $\mu$ , diameter of polar capsules 6 $\mu$ .

## CERATOMYXA AGGLOMERATA Davis

[Fig. 63]

1917 *Ceratomyxa agglomerata*

Davis

1917 : 228

Habitat: Gall-bladder of *Synodus foetans*; Beaufort.

Vegetative form: Pyriform, usually with long, slender, posterior process. Body colorless and transparent. Actively motile, moving by means of characteristic wavelike movements of the ectoplasm, from which are projected numerous short, conical to filiform pseudopodia. Pseudopodia travel back along sides of body for about one-third its length and then disappear, new ones being continually formed at the anterior end. Ectoplasm distinguishable at anterior end. Endoplasm clear, very transparent, usually homogeneous, sometimes finely granular. Large numbers of fat globules usually present. Size of sporulating trophozoites 38 $\mu$  by 12 $\mu$ . Disporous.

Spore: Asymmetrical, one valve being smaller and more attenuated than the other; larger valve compressed. Polar capsules spherical. Coiled polar filaments indistinct. Sporoplasm filling nearly entire smaller valve, but only extending a short distance into the larger one. Dimensions: breadth 24 to 28 $\mu$ , sutural diameter 5 $\mu$ , diameter of polar capsules 3 $\mu$ .



## CERATOMYXA AMORPHA Davis

[Fig. 64]

1917 *Ceratomyxa amorpha*

Davis

1917 : 228

Habitat: Gall-bladder of *Synodus foetans*; Beaufort.

Vegetative form: Rounded or irregular in shape, with short lobose pseudopodia; not pyriform; slowly ameboid. Body colorless. Ectoplasm well developed, forming a distinct layer; transparent, finely granular. Endoplasm granular, with large numbers of small fat globules scattered through it or aggregated into one or two large clumps (difference between the present form and *C. agglomerata*). Disporous.

Spore: Asymmetrical; crescent-shaped; valves short, conical, somewhat compressed. One valve distinctly smaller and more conical than the other. Sutural ridge perpendicular to longitudinal axis. Polar capsules large, opening at some distance from the anterior side. Coiled polar filaments distinct. Sporoplasm granular, asymmetrically situated, being chiefly confined to smaller valve. Dimensions: breadth  $27\mu$ , sutural diameter  $11\mu$ , diameter of polar capsules  $4\mu$ .

## CERATOMYXA MONOSPORA Davis

[Figs. 65 to 67]

1917 *Ceratomyxa monospora*

Davis

1917 : 228-229

Habitat: Gall-bladder of *Peprilus alepidotus*; Beaufort. Abundantly present in June, much less in July, being entirely absent in the bladder at the end of the month.

Vegetative form: Pyriform, with a slender posterior process and one to several filiform pseudopodia at anterior end. Body colorless and transparent. Movements very slow. No clear differentiation between ectoplasm and endoplasm, the entire body being composed of a clear, finely granular protoplasm. Fat globules more abundant in larger individual, which are aggregated into small clumps. Size of vegetative trophozoites up to  $24\mu$  in length and  $15\mu$  in width. Monosporous form much smaller than disporous. Monosporous and disporous. Nearly entire substance of trophozoite is used up in spore formation.

Spore: Crescent-shaped. Valves cylindrical, tapering toward the end, which is rounded and compressed. Curvature of valves varies. One valve is more attenuated than the other. Sutural ridge perpendicular to the longest diameter. Polar capsules large. Sporoplasm usually asymmetrically situated. Dimensions: breadth 18 to  $25\mu$ , sutural diameter 5 to  $6\mu$ , diameter of polar capsules  $3\mu$ .

Remarks: This species is evidently very close to *C. pallida* Thél. Similar form was found in *Prionotus evolans* (gall-bladder), which showed somewhat larger trophozoites and spores than *C. monospora*.

## CERATOMYXA STREPTOSPORA Davis

[Figs. 68 and 69]

1917	<i>Ceratomyxa streptospora</i>	Davis	1917 : 229
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Habitat: Gall-bladder of *Chaetodipterus faber*; Beaufort (June, but not in July).

Vegetative form: Pyriform, colorless and transparent. A few conical, filiform, wavelike pseudopodia at anterior end. Ectoplasm recognizable at anterior end. Endoplasm finely granular, with a few, small, fat globules, filled with transparent, homogeneous spherules. Size: 48 by 12 $\mu$  to 60 by 9 $\mu$ . Disporous.

Spore: Compressed valves greatly elongated, with rounded ends. Sutural ridge. Polar capsules spherical. Coiled polar filament indistinct. Sporoplasm finely granular, entirely filling both valves. Dimensions: breadth 34 to 39 $\mu$ , sutural diameter 4 $\mu$ , diameter of polar capsules 3 $\mu$ .

## CERATOMYXA AGGREGATA Davis

[Fig. 70]

1917	<i>Ceratomyxa aggregata</i>	Davis	1917 : 229
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Habitat: Gall-bladder of *Leostomus xanthurus*, *Micropogon undulatus*; Beaufort (July).

Vegetative form: Form rounded to somewhat irregular in shape, rarely pyriform; slowly ameboid. Body colorless and transparent. No clear differentiation of protoplasm. Endoplasm finely granular, containing numbers of small fat globules. Sporulating trophozoites show a tendency to collect in groups composed of a large number of individuals so closely associated that it is often impossible to make out the individual outlines. Size of full-grown form 18 $\mu$  by 14 $\mu$ . Disporous.

Spore: Crescent-shaped; valves much elongated, tapering toward the ends, which are compressed. Polar capsules spherical and opaque. Sporoplasm granular, situated symmetrically in the spore cavity. Dimensions: breadth about 50 $\mu$ , sutural diameter 6 to 7 $\mu$ , diameter of polar capsule 3.5 $\mu$ .

## CERATOMYXA UNDULATA Davis

[Fig. 71]

1917	<i>Ceratomyxa undulata</i>	Davis	1917 : 230
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Habitat: Gall-bladder of *Ancylopesetia quadrocellata* Gill.; Beaufort (June to August).

Vegetative form: Pyriform, sometimes fusiform, tapering toward posterior end. Movements rapid. Body colorless. Ectoplasm observable at anterior part, constantly undergoes rapid, wavelike undulating movements and extrudes fine conical or filiform pseudopodia. Pseudopodia

are formed very rapidly and vary in length. After reaching a considerable length the pseudopodia usually travel posteriorly along sides of body and then disappear. Endoplasm very transparent, often vacuolated, containing numerous small fat globules. Size of full-grown trophozoite:  $25\mu$  by 10 to  $12\mu$  in average. Disporous.

Spore: Crescent-shaped. Valves cylindrical, not compressed, ends rounded, one valve being somewhat longer and more conical than the other. Polar capsules convergent. Coiled polar filaments distinct. Sporoplasm granular, asymmetrically situated, sometimes being almost confined to more conical valve. Dimensions: breadth 22 to  $24\mu$ , sutural diameter  $6\mu$ , diameter of polar capsules  $3\mu$ .

### CERATOMYXA NAVICULARIA Davis

[Figs. 72 and 73]

1917    *Ceratomyxa navicularia*    Davis    1917 : 230

Habitat: Urinary bladder of *Paralichthys dentatus*, *P. albiguttus*, *Sphaeroides maculatus*; Beaufort (June to August).

Vegetative form: Rounded or slightly irregular in shape, never pyriform. Body colorless. Very slow ameboid. No distinct ectoplasm. Entire trophozoite finely granular, containing a few small fat globules. Nearly entire body is used up in the formation of spores. Diameter about  $17\mu$ . Disporous.

Spore: Variable in shape and size. Symmetrical or asymmetrical, often boat-shaped, slightly compressed dorso-ventrally, with rounded ends. Polar capsules convergent, shows polar filament indistinctly. Sporoplasm finely granular, extending into both valves, but usually somewhat farther into one than the other. Dimensions: breadth 14 to  $22\mu$  (average  $16\mu$ ), sutural diameter 5 to  $7.5\mu$  (average  $6\mu$ ), diameter of polar capsules  $2\mu$ .

### CERATOMYXA SPINOSA Davis

[Fig. 74]

1917    *Ceratomyxa spinosa*    Davis    1917 : 230

Habitat: Urinary bladder of *Paralichthys albiguttus*; Beaufort.

Vegetative form: Rounded or slightly irregular in shape, with short, lobose pseudopodia; slowly ameboid. Body colorless and transparent. Distinct differentiation of protoplasm along the entire surface, ectoplasm forming outer layer. Endoplasm faintly granular, with numerous small fat globules. Monosporous and disporous.

Spore: Central portion greatly enlarged; ovoid, with very long tapering process extending out from each end. Sutural line perpendicular to the longest diameter. Polar capsules large and spherical. Sporoplasm finely

granular, chiefly located in one valve, extending into the other only a short distance beyond the capsule. Dimensions: breadth  $80\mu$ , breadth of enlarged central portion  $13\mu$ , sutural diameter  $7\mu$ , diameter of polar capsules  $4\mu$ .

Genus MYXOPROTEUS Doflein emend. Davis

1898	<i>Myxoproteus</i>	Doflein	1898 : 287
1917	<i>Myxoproteus</i>	Davis	1917 : 219

The characters of the genus are described on page 56.

Type species: *Myxoproteus ambiguus* (Thélohan) Doflein.

MYXOPROTEUS AMBIGUUS (Thélohan) Doflein

. [Figs. 75 to 80]

1895	<i>Myxosoma ambiguus</i>	Thélohan	1895 : 344
1898	<i>Myxoproteus ambiguus</i>	Doflein	1898 : 287-288

Habitat: Urinary bladder of *Lophius piscatorius*; Le Croisic, Rovigno, Napoli.

Vegetative form: Polymorphous. Color milky white. Protoplasm is filled with numerous granules and fat globules. Pseudopodia, short, pointed lobose. Plasmogamy and plasmotomy take place. Many small individuals formed apparently by plasmotomy, often, make up groups. Disporous, polysporous?

Spore: Almost pyramidal, with anterior processes. Two very large polar capsules at the anterior end. The distance between these capsules is equal to or greater than the diameter of the capsules. Sporoplasm with two nuclei. Dimensions: length  $25\mu$ , breadth 18 to  $20\mu$ , diameter of polar capsules  $7\mu$ .

MYXOPROTEUS CORDIFORMIS Davis

[Figs. 81 to 83]

1917	<i>Myxoproteus cordiformis</i>	Davis	1917 : 231
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Habitat: Urinary bladder of *Chaetodipterus faber*; Beaufort (June, July).

Vegetative form: Rounded; very slowly ameboid, usually forming a single, short, lobose pseudopodium. Body colorless and transparent. Ectoplasm not distinct. Entire trophozoite finely granular, with a few fat globules. Rarely vacuolar. Small trophozoites often show a single large, central vacuole. Rounded sporulating trophozoites  $18\mu$  in diameter. Disporous.

Spore: Heart-shaped in front view, with peculiar wing-like expansions on each side which contain remains of parietal cells. Sutural plane oblique in position. Capsulogenous cells distinct. Sporoplasm finely granular, fills the extracapsular cavity of the spore. Dimensions: length  $12\mu$ , breadth 10 to  $11\mu$ , thickness  $6\mu$ , polar capsules 3 to  $4\mu$  in diameter.

### MYXOPROTEUS CORNUTUS Davis

[Fig. 84]

1917 *Myxoproteus cornutus*

Davis

1917 : 231

Habitat: Urinary bladder of *Bairdiella chrysura*; Beaufort.

Vegetative form: Somewhat elongated or irregular in shape, with short lobose pseudopodia; slowly ameboid. Differentiation of protoplasm clear. Ectoplasm well developed, hyaline; in rounded individuals forming a distinct layer around the body. Endoplasm opaque, contains coarse refringent granules varying in shape, and a few fat globules. In contracted rounded resting condition, endoplasm becomes condensed, while ectoplasm appears more abundant. Rounded trophozoites up to  $27\mu$  in diameter. Disporous.

Spore: Heart-shaped, with two anterior processes. Shell very thick. Polar capsules large, opening some distance apart. Coiled polar filament distinct. Sporoplasm finely granular, with a few small fat globules, fills the extracapsular cavity of the spore. Dimensions: sutural diameter exclusive of the processes  $9\mu$ , breadth  $12\mu$ , length of processes  $5\mu$ , diameter of polar capsules  $3\mu$ .

### Genus WARDIA nov. gen.

The characters of the genus are described on page 56.

Type species: *Wardia ovinocua* nov. spec.

### WARDIA OVINOCUA nov. spec.

[Figs. 85 to 95]

Habitat: Ovum and connective tissue of ovary of *Lepomis humilis* Girard;\* Salt Fork, Ill. (November). Only one fish, 6.5 cm. long with normal appearance, was found to be infected.

Vegetative form: Trophozoites form cysts visible to the naked eyes as white spherical spots in the pink-colored ovary. Four cysts present. The cyst (Figs. 85 and 86), in section, shows a circular form surrounded by several layers of hypertrophied nurse cells and connective tissue, in which many large blood vessels are present. Protoplasm is not clearly differ-

\*Professor F. Smith of the Department kindly identified all the fish that were collected in the vicinity of Urbana and mentioned in this paper as hosts, for which the writer wishes to express his appreciation.

entiated into ectoplasm and endoplasm, the whole protoplasm showing granulated reticular structure. Cysts contained numerous fully developed spores and a small number of spores in developmental stages, which suggested the fact that two spores rise from each pansporoblast. The parasite is also found in the state of diffuse infiltration in the connective tissue around the cyst. Diameter of cysts 316 to 445 $\mu$  in sections. Polysporous.

Spore: In front view, isosceles triangular form, two sides of which usually convex, with more or less attenuated anterior end (Figs. 87, 90, 92); in profile, ellipsoidal (Fig. 88); and oval viewed from the anterior end (Fig. 89). Sutural plane at right angles to the longest diameter (Figs. 87 and 89). Shell comparatively thin except at the anterior end and has many fine network-like ridges on the surface. These ridges are hardly observable on fresh spores on account of their fine form and the conspicuously large polar capsules lying in the spore. When stained, however, they are not only made distinctly visible, but the prolongation of each ridge from the posterior edge which forms about 1 $\mu$  long fringe-like structure is also more clearly recognized (Figs. 90–95). Two large and spherical polar capsules located in the central portion of the spore. Coiled (5 to 6 times) polar filament extremely distinct. The openings of polar capsules at the anterior end. Sporoplasm comparatively small, finely granular, without any vacuole, contains two small nuclei, when stained. Dimensions in vivo: sutural diameter 9 to 10 $\mu$ , breadth 10 to 12 $\mu$ , thickness 6 $\mu$ , diameter of the polar capsule 4 $\mu$ , length of polar filament 35 to 45 $\mu$ .

#### WARDIA OHLMACHERI (Gurley) Kudo

[Figs. 96 and 97]

1893	<i>Myxosporidian</i>	Ohlmacher	1893 : 561–567
1893	<i>Chloromyxum ohlmacheri</i>	Whinery	1893 : 660–662
1894	<i>Chloromyxum (Sphaerospora)</i> <i>ohlmacheri</i>	Gurley	1894 : 267–272
1895	? <i>Leptotheca ranae</i>	Thélohan	1895 : 383
1899	<i>Leptotheca ohlmacheri</i>	Labbé	1899 : 87

Habitat: Urinary tubules of kidney of *Bufo lentiginosus* Shaw and kidney of *Rana esculenta* and *R. temporaria* (*R. fusca*); Sycamore, De Kalb county, Ill.

Vegetative form: Not found.

Spore: Transversely elliptic. Sutural plane perpendicular to the longer axis of the spore. A well defined undulate-parallel longitudinal striation on the shell. Sutural ridge comparatively well marked. Two polar capsules lying side by side, occasionally only one. Dimensions: sutural diameter 6 $\mu$ , breadth 8 $\mu$ , diameter of polar capsule 3 to 3.5 $\mu$ , length of polar filament 6 to 8 times the breadth of spore (48 to 64 $\mu$ ).

Remarks: This form is apparently very much different from any species of genus *Leptotheca*, in the general form, form of polar capsules,

striations on the shell and the habitat. Tho the form of the spore is different from the type species of the genus *Wardia* and nothing is known about the vegetative form, the presence of large spherical polar capsules in the central portion of the spore, the striations on the shell and the occurrence of the same nature, i.e., from fresh waters in the close-by localities, show its nearer relationship to the genus *Wardia* than to the genus *Leptotheca*. Hence it is placed here provisionally.

Genus MITRASPORA Fujita emend. Kudo

1912 *Mitraspora* Fujita 1912 : 259-260

The characters of the genus are described on page 56.

Type species: *Mitraspora cyprini* Fujita.

MITRASPORA CYPRINI Fujita

[Figs. 98 to 104]

1912 *Mitraspora cyprini* Fujita 1912 : 259-260

Habitat: Renal tubules of kidney and ureters of *Cyprinus carpio* L. and *Carassius auratus* L.; Sapporo (winter), Tokio (March).

Vegetative form: Fujita's only description is as follows: "The sporoblast contains generally three or four spores." The present writer observed a similar form in the ureter and the renal tubule of the kidney of *Cyprinus carpio* L., in Tokio. The observations are as follows: Trophozoites small ameboid (Fig. 98). Body colorless. Movements tardy. Differentiation of protoplasm imperfect. The hyaline ectoplasm recognizable at one side of the body, where lobose pseudopodia are formed (Figs. 98-99). Endoplasm granular with vacuoles and brownish granules, which become larger as the body grows. Size 10 to 40 $\mu$ . Disporous (Kudo) and polysporous (? , Fujita).

Spore: Fujita's descriptions are as follows: Form resembles monk's hood, slightly attenuated at its anterior end. Shell uniformly thin, except at two points of the truncated posterior end. Each shell valve has eight distinct striations which run longitudinally and turn into long cilia up to 5.8 $\mu$  long, planted in a single row at the posterior end of the spore. Two polar capsules at the anterior end. The nucleus is obscure and no vacuole is present. Dimensions: length 10 to 13 $\mu$ , breadth 5 $\mu$ , polar capsules 3.8 $\mu$  by 2 $\mu$ , length of polar filament 15 $\mu$  (weak glycerine). The writer observed the following facts: More rounded with rounded anterior end in front and side views. Shell more or less thick along the entire posterior margin. Striations on shell, variable in number. Sporoplasm granular, without any vacuole, exhibits two nuclei when stained. Posterior filaments 5 to 6 in number and 5 to 6 $\mu$  long, being absent in some spores. Dimensions in vivo: length 10 $\mu$ , breadth 8 to 9 $\mu$ , thickness 6 to 8 $\mu$ , polar capsule 4 $\mu$  by 1.5 to 2 $\mu$ , length of polar filament 35 to 40 $\mu$ .

Remarks: Tho Fujita does not describe the vegetative form and there are some differences in the form and size of the spore between the forms, the writer does not find out any objection against the union of the above mentioned two forms.

### MITRASPORA CAUDATA (Parisi) Kudo

[Figs. 105 to 107]

1910	<i>Sphaerospora caudata</i>	Parisi	1910 : 253-254
1912	<i>Sphaerospora caudata</i>	Parisi	1912 : 289
1913	<i>Sphaerospora caudata</i>	Parisi	1913 : 396-402

Habitat: Renal tubules of kidney of *Alosa finta* Cuv. var. *lacustris* Fatio; Lake Como.

Vegetative form: Rounded or variously elongated owing to the movements. Protoplasm is distinctly differentiated into ectoplasm and endoplasm. Ectoplasm, hyaline and homogeneous, forms slowly moving lobose pseudopodia. Endoplasm granular, contains yellow globules and fat granules. Disporous and polysporous.

Spore: Subspherical in front view; oval in profile; anterior end being more rounded than the posterior end. Shell rather thick, longitudinally striated. In front view, the posterior end enlarged into a quadrangular form, which appears as a small spine in side-view and which projects backward long and fine filaments, usually six in number. Two well developed polar capsules open on each side of the sutural plane. Polar filament coiled 5 to 6 times. Sporoplasm without any iodophilous vacuole. Dimensions: external length 10 to 11 $\mu$ , internal length 7 to 9 $\mu$ , length of polar capsules 4 to 4.5 $\mu$ , length of polar filament up to 48 $\mu$ , length of posterior filaments up to 28 $\mu$ .

### MITRASPORA ELONGATA nov. spec.

[Figs. 602 to 621]

Habitat: In the urinary tubules and tissue of kidney of *Lepomis cyanellus*; Crystal Lake, Urbana, Ill. From June to July, all the fish examined, 36 in number and 10 cm. in average length, were found to be infected. Other fish such as *Lepomis pallidus* and *Lepomis humilis*, caught at the same time, were free from the infection. Early in June, the number and size of the parasites in a host body were rather small and only a small number of spores could be recognized in the fresh state with the addition of potassium hydrate solution. The growth of the parasite was rather remarkable during the hot weeks in the latter part of June and July so that every fish caught on July 17th showed a heavy infection, exhibiting small whitish pustules over the surface of the organ. During June, vegetative forms and spores were found in the lumen of the urinary tubules,



altho some contained the parasitic masses in the tissue. About the middle of July, the parasite forms conspicuous cysts in the tissue thruout the organ. The cyst may or may not be covered by a thick layer of connective tissue from the host. Aside from this hypertrophy, the host did not show any pathological change which could be recognized.

**Vegetative form:** Youngest trophozoite found in the urinary tubule is multinucleate, rounded, and of from 20 to 50 $\mu$  in diameter. The protoplasm is not differentiated, the entire body is finely granular or coarsely reticular in structure. In the protoplasm are to be seen nuclei and sporoblasts at different stages of development. The union of two propagative cells similar to that of *Myxobolus toyamai* produces a small body which developes into a single sporoblast and ultimately into a single spore (Figs. 605-613). In later stages, the trophozoite reaches a size of 200 $\mu$  in diameter showing many stages of spore formation and mature spores, surrounded by thick layers of connective tissue from the host. Poly-sporous.

**Spore:** Elongated oblong with pointed anterior and truncated posterior extremities. The width is often greatest at the middle of the polar capsules, the posterior portion is much narrower than the anterior. Nearly circular in the cross-section thru the polar capsules. The shell is thin, the sutural line being faintly marked in fresh state. It generally is obliquely located in relation to the capsules. The shell also shows fine longitudinal striations, 14 to 16 in number, on each valve. The sutural line as well as the striations are best seen in spores stained with Heidenhain's iron hematoxylin. Two polar capsules elongated pyriform, mostly equal in size, occupy the anterior half of the spore. Abnormal situations of the polar capsules are sometimes observed (Fig. 619). The coiled polar filament is faintly visible in fresh spores. It is spirally coiled along the wall of the polar capsule without any central axis. This fact was clearly observed in stained section as is shown in Figs. 620 and 621. The filament has seven or eight windings, thus agreeing with the actual length of the extruded polar filament. The polar filament was extruded under the action of potassium hydrate solution. The extrusion takes place even in some spores which were treated with Schaudinn's fixative and kept in 95 per cent alcohol for three months (see the similar observations on *Myxobolus discrepans* on page 157). The sporoplasm is finely granular and transparent. When stained, it shows two nuclei in the center or near the posterior part of the body. Dimensions of preserved spores: length 15 to 17 $\mu$ , breadth 5 to 6 $\mu$ , thickness 4.5 to 5.5 $\mu$ , polar capsule 7.5 $\mu$  by 2 $\mu$ , length of polar filament 40 to 50 $\mu$ .

Suborder SPHAEROSPOREA nom. nov.

The definition of the suborder is recorded on page 57.

## Family CHLOROMYXIDAE Thélohan

1892	<i>Chloromyxidées</i>	Thélohan	1892 : 173
1895	<i>Chloromyxidées</i>	Thélohan	1895 : 344

The characters of the family are described on page 57.

## Genus CHLOROMYXUM Mingazzini

1890	<i>Chloromyxum</i>	Mingazzini	1890 : 160
1892	<i>Chloromyxum</i>	Thélohan	1892 : 173-176
1895	<i>Chloromyxum</i>	Thélohan	1895 : 344

The characters of the genus are described on page 57.

Type species: *Chloromyxum leydigi* Mingazzini.

## CHLOROMYXUM LEYDIGI Mingazzini

[Figs. 108 to 113]

1851		Leydig	1851 : 225-234
1852		Leuckart	1852 : 435
1854		Lieberkühn	1854 : 352
1890	<i>Chloromyxum leydigi</i>	Mingazzini	1890 : 160-164
1892	<i>Chloromyxum leydigi</i>	Thélohan	1892 : 166, 169-170
1894	<i>Chloromyxum leydigi</i>		
	<i>Chloromyxum incisum</i>	Gurley	1894 : 259-260
1895	<i>Chloromyxum leydigi</i>		
	<i>Chloromyxum incisum</i>	Thélohan	1895 : 345-346
1898	<i>Chloromyxum leydigi</i>	Doflein	1898 : 292, 310, etc.
1912	<i>Chloromyxum leydigi</i>	Erdmann	1912 : 149-162
1916	<i>Chloromyxum leydigi</i>	Georgévitch	1916a : 3
1917	<i>Chloromyxum leydigi</i>	Davis	1917 : 236-237
1917	<i>Chloromyxum leydigi</i>	Erdmann	1917 : 276-321
1918	<i>Chloromyxum leydigi</i>	Georgévitch	1918 : 182-189

Habitat: Gall-bladder of *Rhina squatina* L., *Spinax spinax* L., *Scyllium canicula*, *S. asterias*, *Raja batis* L., *R. clavata* L., *R. undulata* Lac., *Torpedo narce* Ris., *T. marmorata*, *T. ocellata*, *T. torpedo* L., *Acanthias acanthias* L., *Trygon pastinaca* L., *Dasybatis hastatus*, *D. sabina*, *Pteroplatea maclura* Le Sueur, *Scoliodon terrae-novae*, *Cestracion zygaena*, *C. tiburo*, *Carcharhinus limbatus*; Roscoff, Concarneau, Marseille, Banyuls, Rovigno, Heligoland, Beaufort, Monaco (May), Napoli, Genova. Erdmann observed the species at Naples from March to August. She noticed mixed infection with *Ceratomyxa reticulata* and especially with *Leptotheca parva*. Georgévitch studied the parasite at Monaco from February to April.

Vegetative form: Polymorphous, being spherical, oval or irregular. The change of the form rather rapid under favourable conditions. Differentiation of protoplasm distinct. Ectoplasm with pseudopodia of various form, i.e., lobose, filiform or intermediary; short, pointed or branched. Endoplasm alveolar, filled with yellowish granules. Doflein observed the plasmodic multiplication of young trophozoites. Polysporous. Erdmann's observations (1917) may be summarized as follows: Ameboid.

Color of the body greenish to dark green. The protoplasm is clearly differentiated into ectoplasm and endoplasm. The ectoplasm is hyaline and covers the entire surface of the body. It appears as a fine fibrous structure when fixed with Bouin's solution. The endoplasm contains besides nuclei, two kinds of spherules; one smaller and yellowish "color-carriers" and the other larger and light to dark greenish reserve bodies. The color-carrier is in part composed of myelin, while the reserve body is of glycogenous nature. The infection was studied experimentally *per os*: young trophozoites appeared in 3 to 5 days which continued to 10th day, various trophozoites were seen in 13 to 19 days, and sporulating individuals were first recognized in 39 days after the infection. The trophozoite multiplies in number either by fission or by budding. It usually contains enclosures which seem to be degenerating erythrocytes. Mictosporous.

Spore: Ovoidal. Shell-valves show wide edge at sutural plane, which is attenuated at the anterior end and forms a quadrilateral process at the posterior end, from which a row of cilia grows. Shell-valves have ridges (6 to 7), which run parallel to the posterior margin. The striations may vary considerably. Four polar capsules at the anterior end. Dimensions: length  $8\mu$ . Erdmann gave the following dimensions: Spores from *Torpedo marmorata* and *T. ocellata*: length 6 to  $9\mu$ , breadth  $5\mu$ , polar capsule  $3\mu$  by  $2\mu$ . Those from *Scyllium asterias*: length 8 to  $9\mu$ , breadth  $6\mu$ , polar capsule  $2\mu$  by  $1\mu$ . Those from *Raja batis*: length 7 to  $8\mu$ , breadth  $5\mu$ , polar capsule  $2\mu$  by  $1\mu$ . Length of polar filament 20 to  $30\mu$  (absolute alcohol warmed up to  $40^{\circ}\text{C}$ .).

### CHLOROMYXUM CAUDATUM Thélohan

[Fig. 114]

1895    *Chloromyxum caudatum*    Thélohan    1895 : 346

Habitat: Gall-bladder of *Molge cristata* Laur.; Vicinity of Rennes.

Vegetative form: Body yellowish with lobose pseudopodia. Protoplasm finely granular.

Spore: Oval or spheroidal. Shell enlarged at the anterior part, having a simple or bifurcated tail-like process, as in Henneguya, at the posterior end. Dimensions: total length  $18\mu$ , length  $8\mu$ , breadth 6 to  $7\mu$ , length of tail  $10\mu$ .

### CHLOROMYXUM QUADRATUM Thélohan

[Figs. 115 to 117]

1891		Pfeiffer	1891 : 111
1893		Pfeiffer	1893 : 81
1895	<i>Chloromyxum quadratum</i>	Thélohan	1895 : 347
1912	<i>Chloromyxum quadratum</i>	Parisi	1912 : 289
1913	<i>Chloromyxum quadratum</i>	Awerinzew	1913a : 155
1913	<i>Chloromyxum quadratum</i>	Fermor	1913 : 199

Habitat: Muscle of *Syngnathus acus* L., *Trachurus trachurus* L., *Nerophis aequorens* L., *Callionymus lyra* L., *Coris julis* L., *Ariodes polystaphylodon*, kidney of *Blennius gattorugine* Brunn; Helder, Roscoff, Concarneau, Marseille, Beira (Africa), Napoli (summer).

Vegetative form: Not described by any of these authors.

Spore: Quadrangular pyramid with curved edges and roundish angles. Four polar capsules at the anterior end. Dimensions: length  $6\mu$ , breadth  $5\mu$ , length of polar filament 8 to  $10\mu$ .

### CHLOROMYXUM FLUVIATILE Thélohan

[Fig. 118]

1892	<i>Chloromyxum fluvatile</i>	Thélohan	1892 : 173-176
1895	<i>Chloromyxum fluvatile</i>	Thélohan	1895 : 346

Habitat: Gall-bladder of *Leuciscus cephalus* L.; Paris.

Vegetative form: Young trophozoites colorless; adults yellowish. Form highly variable. Active change of the form of body. Clear differentiation between ectoplasm and endoplasm. Ectoplasm usually recognizable at one end of the body where lobose pseudopodia are formed. Size reaches 25 to  $30\mu$ . Polysporous.

Spore: Spherical, generally small. Sutural ridge fairly well marked. Dimensions: 7 to  $8\mu$  in diameter.

### CHLOROMYXUM MUCRONATUM Gurley

[Figs. 119 to 122]

1854		Lieberkühn	1854 : 352-353
1879		Leuckart	1879 : 248
1882		Bütschli	1882 : Pl. 38 : 17
1883		Balbani	1883 : 201, 203
1893	<i>Chloromyxum mucronatum</i>	Gurley	1893 : 419
1894	<i>Chloromyxum mucronatum</i>	Gurley	1894 : 264, 265
1908	<i>Chloromyxum mucronatum</i>	Auerbach	1908 : 456
1909	<i>Chloromyxum mucronatum</i>	Auerbach	1909a : 71

Habitat: Urinary-bladder and kidney of *Lota lota* L.; Bodensee, other localities not mentioned.

Vegetative form: Spherical, elliptical or irregular. Size up to  $75\mu$  in diameter. Protoplasm containing irregularly scattered fat-like globules.

Spore: Sharp-contoured; subglobular, mucronate anteriorly. Dimensions: length  $8\mu$ .

## CHLOROMYXUM DIPLOXYS (Gurley) Thélohan

[Figs. 123 to 125]

1866	Balbani	1866 : 600-602
1867	Balbani	1867 : 275, 276, 335
1882	Bütschli	1882 : 590
1890	Pfeiffer	1890 : 559
1892	Henneguy et Thélohan	1892 : 587
1893	Gurley	1893 : 411
1894	Gurley	1894 : 281
1895	Thélohan	1895 : 347

Habitat: Abdominal cavity of *Tortrix viridana* L. (imago);

Vegetative form: Trophozoites form spherical cysts, 230 to 400 $\mu$  in diameter. Cyst membrane rather thick. Protoplasm containing brownish granules, and fat-like globules (red with iodine).

Spore: Elliptic or slightly flattened. Sutural line straight, forming a ridge. Two polar capsules at each end.

## CHLOROMYXUM PROTEI Joseph

1905	<i>Chloromyxum protei</i>	Joseph	1905 : 450-451
1907	<i>Chloromyxum protei</i>	Joseph	1907 : 398-412

Habitat: Renal tubules of kidney of *Proteus anguineus* L.; Vienna.

Vegetative form: Generally rounded or sausage form. No clear differentiation between ectoplasm and endoplasm. Movements slow. Probable occurrence of plasmotomy by budding and division. Size: 40 to 45 $\mu$  by 28 to 40 $\mu$ .

Spore: Spherical. Shell finely striated parallel to the sutural line. Four polar capsules each with an independent opening. Dimensions: 10 to 13 $\mu$  in diameter, polar capsules 4 to 6 $\mu$  long. The polar filament appears to be rather short.

## CHLOROMYXUM TRUTTAE Léger

[Fig. 126]

1906	<i>Chloromyxum truttæ</i>	Léger	1906 : 267-270
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Habitat: Gall-bladder and gall-duct of *Trutta fario* L.; Dauphiné.

Vegetative form: Ameboid form. Elongated. Form resembles an *Amoeba limax* of about 40 $\mu$  in length. Roundish or irregularly contoured, with small pseudopodia. Ovoidal or spherical, 25 to 40 $\mu$  in diameter without any visible pseudopodia (resting state). Body colorless, clear and hyaline. Very active movements which last for several hours after the death of the host. Broad and obtuse pseudopodia well developed at the anterior end of the body. Endoplasm alveolar, contains variable numbers of nuclei, which are seen *in vivo*, refractive bodies and chromatic granules. Monosporous(?) and polysporous.

Spore: Spherical. Four polar capsules of different size. Shell-valves marked with parallel ridges. Dimensions: 8 to 9 $\mu$  in diameter.

## CHLOROMYXUM CRISTATUM Léger

[Figs. 127 and 128]

1906	<i>Chloromyxum cristatum</i>	Léger	1906 : 270-272
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Habitat: Gall-bladder of *Tinca vulgaris* Cuv.; Grenoble.

Vegetative form: Ordinarily massive, with oval or round contours, without noticeable pseudopodium. Ectoplasm hyaline. Endoplasm granular and colorless. Average diameter of the adults about 20 $\mu$ . Monosporous, rarely disporous.

Spore: Spherical or subspherical. Ten marked ridges run anteroposteriorly on each shell-valve, so that it presents a cog-wheel form in cross section. Four polar capsules at the anterior end, one pair being smaller than the other. Sporoplasm with two nuclei. Dimension: 10 to 11 $\mu$ .

## CHLOROMYXUM DUBIUM Auerbach

[Figs. 129 to 133]

1908	<i>Chloromyxum dubium</i>	Auerbach	1908 : 456-459
1910	<i>Chloromyxum dubium</i>	Auerbach	1910c : 177

Habitat: Gall-bladder of *Lota vulgaris* Cuv.; Bodensee (April to September).

Vegetative form: Spherical or rounded. Rarely irregular forms. Protoplasm is differentiated distinctly into ectoplasm and endoplasm. Ectoplasm very thin, forms pseudopodia which move slowly. Endoplasm granular, contains fat globules. Majority of the trophozoites appear to live floating in the bile, while some are attached to the epithelium of the bladder. Disporous and polysporous.

Spore: Spherical, with four polar capsules. Each shell valve has longitudinal ridges, variable in number (6 ridges are found on the drawing), which run parallel to the sutural line. Four polar capsules of nearly same size and convergent. Sporoplasm finely granular with two nuclei. Dimensions: diameter 10.8 $\mu$ , length of polar capsule 3.6 $\mu$ .

## CHLOROMYXUM sp. Awerinzew

[Fig. 134]

1908	<i>Chloromyxum</i> sp.	Awerinzew	1908 : 43, 47, 48
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Habitat: Gall-bladder of *Raja radiata*; Murman coast?

Vegetative form: Form rounded. The protoplasm is distinctly differentiated into ectoplasm and endoplasm. Ectoplasm hyaline and comparatively abundant in quantity compared with endoplasm, forms lobose pseudopodia of active movements. Endoplasm vacuolated, contains enclosures. Between the two layers, a thin layer of protoplasm, reticular in structure and stained deeply with hematoxylin, is present.

Spore: No figure.

## CHLOROMYXUM THYMALLI Lebzelter

1912 *Chloromyxum thymalli* Lebzelter 1912 : 295-296Habitat: Gall-bladder of *Thymallus thymallus* L.; Vienna?

Vegetative form: Irregular form, 33 to 35 $\mu$  long in average. Endoplasm contains fat globules which stain brown with carmine. Trophozoites attached to the epithelium. In average, 6 spores formed in each individual. Intracellular stage in the epithelial cell is supposed. Polysporous.

Spore: Spherical. Shell structure similar to *C. protei*, but ridges are more developed and exhibit somewhat wavy courses. Polar capsules of equal size. Dimensions: 9 to 9.5 $\mu$  in diameter, polar capsules 3 $\mu$ .

## CHLOROMYXUM KOI Fujita

[Fig 135]

1913 *Chloromyxum koi* Fujita 1913 : 257-259Habitat: Gall-bladder of *Cyprinus carpio* L.; Sapporo (Nippon).

Vegetative form: Spherical, with greatest diameter up to 50 $\mu$ , containing 1 to 3 spores. Each spore is situated in a clear space surrounded by a membranous envelope (sporoblast?), around which there is some finely granular matter (endoplasm?).

Spore: Spherical, exhibiting a somewhat angular contour at the anterior end. Shell thick and has well marked ridges on the surface, i.e., 4 to 5 circular ridges and on both sides of these ridges, two more ridges each bent in a loop-like manner, so that the outline of spore in cross section, is very much like of a toothed wheel with nearly equidistant teeth, 16 to 18 in number. Four polar capsules, two slightly larger than the other two. Dimensions: length 16 $\mu$ , breadth 10 $\mu$ , length of polar capsule 4 $\mu$ , length of polar filament 64 $\mu$ .

## CHLOROMYXUM MAGNUM Awerinzew

[Figs. 136 to 138]

1913 *Chloromyxum magnum* Awerinzew 1913 : 155-156

Habitat: Gall-bladder of *Acanthias blainvillei*;\* Algoa Bay, East London, Lüderitzbucht (Africa).

Vegetative form: Ameboid. Body yellowish by the presence of large yellowish granules in endoplasm. Often round or rosary form. Pseudopodia sometimes absent, so that the trophozoites move like *Amoeba limax* with a cluster of small, hairy pseudopodia at the posterior end. In larger form, small round pseudopodia, composed of homogeneous ectoplasm, are formed. Plasmotomy by budding, was often observed. Usually polysporous, rarely monosporous.

Spore: Elongated spherical form. Four polar capsules at the narrow, anterior end. Sporoplasm with two nuclei. Dimensions: length 40 to 48 $\mu$ , breadth 30 to 38 $\mu$ , length of polar capsules 12 to 15 $\mu$ .

\* Misprinted in Awerinzew's paper as *blainvillei*.

## CHLOROMYXUM FUNDULI Hahn

[Figs. 139 and 140]

1915 *Chloromyxum funduli* Hahn 1915 : 205-206

Habitat: Muscle of *Fundulus* sp.; Woods Hole. In one fish.

Vegetative form: Hahn made observations on few fresh and stained smears. According to him, it is clear that the staining was abnormal. It is hard to quote this here as he used different terms without giving any definition. The reader is advised to consult Hahn's paper.

Spore: Form slightly resembles that of *Choloromyxum quadratum*. Posterior end rounded, the anterior portion narrow and truncated at the tip; optical cross-section thru the posterior part of the polar capsules, circular. Four polar capsules at the anterior end. Dimensions: height (length)  $6\mu$ , breadth and thickness  $7.5\mu$  respectively.

Remarks: As to the comparison of the present species with *Chloromyxum clupeiidae* Hahn, see p. 94.

## CHLOROMYXUM MISGURNI Kudo

[Figs. 141 to 146]

1916 *Chloromyxum misgurni* Kudo 1916 : 6-7

Habitat: Gall-bladder of *Misgurnus anguillicaudatus* Cantor; Tokio (September).

Vegetative form: Round or irregular. Semicircular when viewed from side. From the flat surface, many fine root-like, filiform pseudopodia are extruded. No clear differentiation between ectoplasm and endoplasm. Endoplasm alveolar. Trophozoites always found attached to the lining epithelial cells. Size up to  $50\mu$  by  $20\mu$ . Polysporous (6 to 8 spores), rarely disporous.

Spore: Spherical, slightly attenuated at the anterior end. Sutural line straight and forms a ridge. Fine longitudinal striations run parallel to the sutural line. Four polar capsules at the anterior end. Sporoplasm finely granular, has two nuclei of equal size. Dimensions: length 8 to  $9\mu$ , breadth 6 to  $7\mu$ , thickness 5 to  $6\mu$ , length of polar capsule 2 to  $3\mu$ , of polar filament 28 to  $35\mu$  (KOH).

Remarks: The host is often infected at the same time by *Chloromyxum fujitai*, the trophozoites of which can be distinguished from the present form by the structure and the floating habit in the bile. Spores in the two species are decidedly different in form, structure and size.

## CHLOROMYXUM FUJITAI Kudo

[Figs. 147 to 152]

1916 *Chloromyxum fujitai* Kudo 1916 : 7-9

Habitat: Gall-bladder of *Misgurnus anguillicaudatus* Cant.; Tokio, (5% of the fish examined in September, found infected).



Vegetative form: Round or irregular. No clear differentiation of protoplasm. Endoplasm highly vacuolated. Ectoplasm being hardly distinguishable. Size up to  $40\mu$  in diameter. Trophozoites float in the bile in almost all cases. Disporous and polysporous (up to 8 spores).

Spore: Spherical, often attenuated at the anterior end. Sutural line not straight. Shell very thick, shows thick ridges running longitudinally on the surface. In optical cross section, the spore presents an outline like a cog-wheel with 20 to 22 ridges. The thickness of ridges varies regularly; the thickest ones being located on two lines where a plane perpendicular to sutural plane cuts the shell longitudinally, others decreasing in thickness as they approach the sutural line. Four polar capsules at the anterior end. Sporoplasm with two nuclei. Dimensions: length 10 to  $12\mu$ , breadth 8 to  $10\mu$ , polar capsules 2 to  $3\mu$ , length of polar filament 23 to  $30\mu$  (KOH).

### CHLOROMYXUM CLUPEIDAE Hahn

[Figs. 153 to 156 and 562 to 565]

1900	Sporozoa	Tyzzar	1900 : 66-68
1901	Sporozoa	Linton	1901 : 438
1910	<i>Chloromyxum</i> sp.	Auerbach	1910 : 178
1917	<i>Chloromyxum clupei</i> dae	Hahn	1917 : 13-19

Habitat: Body musculature of *Clupea harengus*, *Pomolobus pseudoharengus*, *P. aestivalis*, *P. mediocris*, *Brevoortia tyrannus*, *Stenotomus chrysops*, *Tautoglabrus adspersus*; Woods Hole.

Tyzzar mentioned in his paper and also in a letter to the writer that he collected the material in August of 1900 and that he found the infection occurred only among young fish. Hahn also called attention on the latter fact.

Vegetative form: Hahn's observations are as follows:

Clusters of spores ("pseudocysts") are spindle-shaped, especially when young, usually lying between the bundles of muscle fibres. Color white or creamy. Larger ones usually "in pocket just beneath the integument." Schizogonic multiplication probably exists. Parasites hard to stain, anilin dyes being unable to stain at all. Large form (probably composed of many individuals)  $890\mu$  by  $30\mu$ .

Tyzzar described as follows: Cysts up to 1 to 2 mm. in length, lying between the muscle fibres of the myotomes, surrounded at times by membranous connective tissue. The parasites also occur in diffused infiltration.

Linton found two cysts, 1.74mm. by 1.16mm. and 1.16mm. by 0.58mm. and also diffused state between the fibrillae.

The writer's observation on slides prepared by Dr. Tyzzar\* is as follows: Two cysts in sections; one almost spherical,  $480\mu$  by  $430\mu$ , sur-

\*The writer had recently the opportunity of examining the slides of the parasites prepared by Dr. Tyzzar, which occasion he appreciated very much. As a result of this, the writer became convinced of the identity of forms observed by Tyzzar, Linton and Hahn, tho he could not examine the latter authors' specimens.

rounded by several layers (about  $10\mu$  thick) of connective tissue of the host, the other oval,  $120\mu$  by  $110\mu$ . The staining sufficed to reveal only indistinct structure of the parasites. The homogeneous ectoplasm surrounds the entire surface of the body as a uniform, but very thin layer. Endoplasm granular, filled with spores of remarkably identical stages of development. Isolated spores, also, occur in the muscle bundle in the state of diffused infiltration. Polysporous.

Spore: Hahn describes it as follows: Low conical pyramid with round base; square with bulging sides. No indication of valves in the spore shell. Dimensions: height (length)  $5\mu$ , breadth and thickness  $7\mu$ , polar capsule  $2\mu$  by  $1\mu$ .

Linton's form: squarish in outline with rounded corners,  $7\mu$  in diameter.

Tyzzer describes his form as follows: Quadrilateral in anterior end view; oval in side view. The four corners are a little protuberant and are directed slightly forward. Shape varies considerably in different species of host. The corners of the spore from *Stenotomus chrysops*, are greatly drawn out, exhibiting stellate form. Four polar capsules radiating from the anterior extremity toward the four corners. Shell shows four furrows radiating from the anterior extremity outwards to the side. Sporoplasm occupies extracapsular cavity. Polar filaments are extruded under the action of acetic acid. Dimension: breadth 7 to  $7.5\mu$ .

The writer's observations are as follows:

Spores in fixed and decolorized smears. In smear, most of the spores are seen lying on the base exposing the anterior end view toward the observer's eyes, a few lying with the sutural diameter parallel to the surface of the slide. Form quadrilateral with corners more or less drawn out in anterior end view; oval, with concave posterior side in front view (Figs. 562 to 564). Shell apparently thin but was not clearly separated from the sporoplasm which is finely granular and fills the extracapsular cavity of the spore. Four polar capsules of nearly same size and pyriform. Coiled polar filament indistinct. When stained, the polar capsules stained deeply. It is remarkable to see almost all of the spores exhibit four deeply stained nuclei of capsulogenous cells, which in ordinary case disappear as the spore matures. Dimensions: height (length) 4 to  $4.75\mu$ , breadth and thickness  $5.4$  to  $6.5\mu$ , polar capsule about  $1.5\mu$  by  $0.75\mu$ .

Remarks: Thus the forms of Tyzzer, Linton and Hahn had better be treated as one and the same species. As to the distinction of *Chloromyxum funduli* and the present species, the writer is unable to make it clear as he could not examine the preparation of the former species and especially as he observed some intermediate forms between these two forms in Dr. Tyzzer's preparations of the present species.

## CHLOROMYXUM GRANULOSUM Davis

[Figs. 157 and 158]

1917 *Chloromyxum granulorum* Davis 1917 : 237

Habitat: Urinary bladder of *Tylosurus marianus*; Beaufort (July, August).

Vegetative form: Elongated when first placed on the slide, but soon becomes contracted and motionless; progressing by very slow ameboid movements. Ectoplasm usually undistinguishable, being noticed only in a few individuals which had formed one or two short, lobose pseudopodia of hyaline ectoplasm. Body colorless to light yellow. After being on the slide for some time rounded trophozoites often became surrounded by a distinct ectoplasmic layer. Entire body usually coarsely granular, the granules varying greatly in size and shape; sometimes indistinctly vacuolated. Fat globules also present. Size of rounded trophozoites about  $30\mu$ . Disporous and polysporous.

Spore: Spherical, with four distinct ridges on the posterior half of each valve converging toward the anterior end. Sutural ridge distinct. Polar capsules pyriform and convergent. Dimensions: diameter  $7\mu$ , polar capsules  $2\mu$ .

Remarks: Trophozoites from some fish were all colorless, while the larger trophozoites from others were distinctly yellow.

## CHLOROMYXUM TRIJUGUM nov. spec.

[Figs. 159 to 182]

Habitat: Gall-bladder of *Lepomis megalotis* Raf.; Stony Creek, and Homer Park, Ill. (November). The parasite was only found in this species, *Lepomis humilis* and *L. cyanellus* seined at the same time being free from the infection. Six specimens, three from each of the above mentioned localities, harboured abundantly both free spores and trophozoites of various stages of development in the bile. The fish, from 6.5 to 10.5cm long, were normal in external appearance and the bladders did not show any particular abnormality, compared with those of other fish, as is usually the case.

Vegetative form: Trophozoites float usually free in the bile, younger forms are most frequently attached to the epithelium of the bladder. Form extremely polymorphous, manifesting various shapes such as, almost circular, rounded, oval, elongated or irregular, which is chiefly due to the active extrusion and retraction of the pseudopodia from the body surface. Body is highly transparent and colorless in both the young and the adult. The differentiation of protoplasm into ectoplasm and endoplasm, is distinctly visible in vivo as well as in stained preparations, especially in larger forms (Figs. 159 to 165). The endoplasm presents an alveolar structure without

any enclosure except the nuclei and various stages of spore formation (Figs. 161, 165, 168 to 171), the alveolar network being smaller at the periphery than in the center. The ectoplasm is a hyaline, transparent and homogeneous layer, free from any coarse granulation in fresh conditions. It shows, however, a very fine reticular structure in stained preparations. The pseudopodia are of two kinds in form, always, formed of ectoplasm alone: the filose and bristle-like form, sometimes branching and protruding from the entire surface or from a localized part of the body, vary in length from 0.5 to 4 $\mu$  according to the size of the individual (Figs. 159, 161, 164). This form developed, sometimes, into a thicker form with two to four branched finer processes. The blunt, lobose pseudopodium formed at a localized part of the body is well recognizable in larger individuals. Frequently the filose and the lobose pseudopodia are formed on a trophozoite at the same time. The movements of the blunt pseudopodia were striking in some specimens. At the beginning of the observation, ten minutes after the bile was removed from the host, two club-shaped pseudopodia (Figs. 161 to 163) which were extruded from a trophozoite, the largest diameter of which being 20 $\mu$ , moved very actively in the semicircular area changing their forms, showing maximum length of 20 $\mu$ . In about thirty minutes, they were retracted and from the same place, a short, oval-shaped pseudopodium was seen to be extruded, which remained in the same position for some time without great change of form (Fig. 164). In another case, a trophozoite with a very broad and rounded pseudopodium extruded actively two to three rounded smaller processes at its extremity (Figs. 165 to 167). After fifteen minutes the pseudopodium was retracted, the ectoplasm forming a uniformly thick layer around the endoplasm. The observations were done at room temperature in hanging drop preparations, sealed with vaseline and paraffin, by using comp. oc. 12 and apo. imm. ob. 2mm., which caused no mechanical pressure upon the parasites. The change of form and especially that of pseudopodia, was clearly observed for one hour and twenty minutes under the above mentioned conditions after the bile was removed from the host. The trophozoites when kept for sixteen hours at room temperature, underwent degeneration and disintegrated, setting free the spores which were formed in them.

No active multiplication by plasmotomy, was observed in vivo. In fixed preparations, however, forms that suggested the occurrence of the process in the present myxosporidian, were recognized. As was stated before, the pseudopodia are always formed of the ectoplasm and as each portion of these dividing forms has many nuclei, the author is inclined to record the presence of plasmotomy in the present form.

Size varies greatly. The monosporous form 10 $\mu$  by 14 $\mu$ , disporous 15 $\mu$  by 25 $\mu$  and polysporous 30 $\mu$  by 50 $\mu$ , the largest individual, developing and containing more than 200 spores, was 300 $\mu$  by 50 $\mu$ .

**Spore:** Generally circular in front view; oval in side view. Shell comparatively thick, consequently the coiled polar filament is frequently indistinct. Sutural ridge straight and distinct. Each valve has a thick straight, sometimes slightly zigzag-form ridge that runs parallel to the sutural line, so that in side view, three distinct ridges encircling the spore are recognized (Figs. 177 and 180). From each of these two ridges, eight to twelve short ridges are directed toward the center of each valve, which can distinctly be observed on the spores stained with Heidenhain's iron hematoxylin (Figs. 179 and 180). They can be seen as faint markings rising from the margin directed toward the center of the spore, in front view of fresh spores. Four pyriform polar capsules of slightly different size open their foramina independently at the anterior end of the spore (Figs. 178 and 181). The sporoplasm, granular and finely reticular, shows almost always two nuclei when stained. Dimensions in vivo: length and breadth 8 to 10 $\mu$ , thickness 5 to 7 $\mu$ , polar capsules 3 to 5 $\mu$  by 2 to 3 $\mu$ , length of polar filament 32 to 40 $\mu$  (H<sub>2</sub>O<sub>2</sub>, KOH).

**Remarks:** In carefully made smear of the bile, a number of empty spores which had been seen in fresh hanging drop preparations, and often spores, in which the sporoplasm with two elongated nuclei seemed to leave the shell (Fig. 182), were recognized. As this particular spore was found close to a thicker mass of the wall of the gall-bladder in the smear, it can hardly be thought that the mechanical pressure during the preparation lead to the mission of the sporoplasm from the spore. It is possible, on the other hand, to think that this is one of the cases of the germination of the spore in the host in which they were developed, as was reported by the author in *Nosema bombycis* Nägeli (Kudo, 1916).

#### CHLOROMYXUM CATOSTOMI nov. spec.

[Figs. 560 and 561]

**Habitat:** Gall-bladder of *Catostomus commersonii* Lac.; Salt Fork, Urbana, Ill. (October). Four fish, from 8 to 14cm.; apparently normal.

**Vegetative form:** Form usually rounded, with filiform pseudopodia. Majority attached to the epithelium, a few being free in the bile. Body colorless. Protoplasm is not well differentiated. Endoplasm occupying the entire body is of granular structure with vacuoles and refringent spherules. Size: from 15 to 35 $\mu$ . When kept for 16 hours in a refrigerator, the trophozoites liberated the spores. The number of spores in each trophozoite is usually 2 or 3, rarely 5 to 6. Active plasmodic multiplication observed when examined. Spores were comparatively small in number, while the trophozoites were attached abundantly to the epithelium of the gall-bladder. Disporous and polysporous.

**Spore:** Form approximately spherical in front view; oval in profile. Shell with very fine striations which run parallel to the sutural ridge that is fairly well marked. Rounded polar capsules almost of same size, have

independent openings at the anterior end. Coiled polar filament indistinct. Abnormal spores with five polar capsules are sometimes seen. Dimensions of fixed spores: length  $8\mu$ , breadth  $7\mu$ , thickness 5 to  $6\mu$ , polar capsules 2 to  $2.5\mu$  by  $1.5\mu$ .

**CHLOROMYXUM WARDI** nov. spec.

[Figs. 632 to 642]

**Habitat:** In the gall-bladder of *Oncorhynchus nerka*: Klutina Lake, Alaska (August). A single gall-bladder collected and preserved in formol by Professor Ward, was found to harbor the present species. The study was done on preserved material and on stained smear preparations.

**Vegetative form:** Young trophozoites (Fig. 632) show ameboid form, and are mostly multinucleated. The protoplasm is not well differentiated either in unstained material or in stained specimens. It is granulated thruout the body, and is vacuolated at places. The smallest form measured was  $18\mu$  in largest diameter. The shape of the body suggests its possession of ameboid movements when alive, altho the writer could not examine fresh specimens. Large trophozoites in which the spore formation had partly been completed are generally rounded with reticular protoplasm. Size varies to some extent. The trophozoite shown in figure 633 contains six mature spores and is  $23\mu$  in largest diameter. The largest one found was 38 by  $30\mu$ , showing ten spores and nuclei. Each spore appears to develop independently from a single sporoblast. Disporous and polysporous.

**Spore:** Rounded pyramidal in front view (Figs. 640 and 641); circular in transverse section (Fig. 638). The shell is thickened near the posterior margin (Figs. 640 and 641). Sutural line is not straight, the ridge being fairly distinct. The striations on the shell vary to a considerable extent (Figs. 634 to 637 and 639). Four polar capsules at the anterior end, mostly unequal in size and shape. The coiled polar filament is invisible in formol material. Potassium hydrate solution does not cause its extrusion in the preserved spores. The sporoplasm is finely granular with two nuclei. Dimensions of unstained preserved spores: diameter 7.5 to  $9\mu$ , polar capsule 3 by  $2.5\mu$ .

**Remarks:** The writer was able to study forty specimens of gall-bladder of Alaskan fishes, chiefly of salmon, which have been collected by Professor Henry B. Ward, during the summer of 1919, for which he wishes to express his deepest appreciation. The examination of these specimens showed that myxosporidia were found only in one of the gall-bladders, and that specimen presented a fairly heavy infection of the present species.

Family SPHAEROSPORIDAE Davis

1917 *Sphaerosporidae*

Davis

1917 : 219

The characters of the family are described on page 57.

## Genus SPHAEROSPORA Thélohan

1892	<i>Sphaerospora</i>	Thélohan	1892 : 167
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The characters of the genus are described on page 57.

Type species: *Sphaerospora divergens* Thélohan.

## SPHAEROSPORA DIVERGENS Thélohan

[Figs. 183 to 186]

1895	<i>Sphaerospora divergens</i>	Thélohan	1895 : 339-340
1912	<i>Sphaerospora divergens</i>	Parisi	1912 : 289
1912	<i>Sphaerospora divergens</i>	Auerbach	1912 : 41-42

Habitat: Urinary tubules of kidney of *Blennius pholis* L., *Crenilabrus melops* L., *C. pavo* Cuv. et V, and urinary bladder of *Hippoglossoides limandoides*; Concarneau, Roscoff, Napoli (July), Smalfjorden.

Vegetative form: Rounded discoidal or spherical or more or less elongate. Ectoplasm transparent, without real pseudopodium. Movements extremely slow. Endoplasm, granular, contains fat globules and small yellowish granules. Size of sporulating individuals: 65 $\mu$  by 55 $\mu$ , 60 $\mu$  by 25 $\mu$ , 60 $\mu$  by 20 $\mu$ , etc. Polysporous (Thélohan); monosporous, and disporous (Auerbach).

Spore: Spherical. Shell with fine striations. Two polar capsules divergent; coiled polar filament visible in fresh state. Sporoplasm fills the extracapsular cavity of the spore. Dimensions: 10 $\mu$  in diameter, often 10 $\mu$  by 12 $\mu$ , the larger diameter coinciding with sutural plane, thickness 8 $\mu$  (Auerbach), polar capsules about 4 $\mu$  long, length of polar filament 20 to 25 $\mu$ .

## SPHAEROSPORA ELEGANS Thélohan

[Figs. 187 and 188]

1890		Thélohan	1890 : 193-209
1892	<i>Sphaerospora elegans</i>	Thélohan	1892 : 167-175
1894	<i>Chloromyxum (Sphaerospora) elegans</i>	Gurley	1894 : 266
1895	<i>Sphaerospora elegans</i>	Thélohan	1895 : 338-339
1909	<i>Sphaerospora elegans</i> *	Auerbach	1909a : 71
1912	<i>Sphaerospora elegans</i>	Parisi	1912 : 289

Habitat: Renal tubules of kidney, connective tissue of ovary and urinary bladder of *Gasterosteus aculeatus* L., *G. pungitius* L., *Lota vulgaris* Cuv., *Phoxinus laevis* L.; Paris, Bretagne, Karlsruhe, Lake Garda.

Vegetative form: Rounded or slightly elongated, not exceeding 20 to 25 $\mu$  in diameter. Protoplasm homogeneous, very finely granular, contains numerous refractive globules, probably of fatty nature. Pseudopodia lobose. Movements slow. Disporous.

\*Misprinted as *Sphaeromyxa elegans*.

Spore: Spherical, somewhat attenuated at the anterior end. Sutural ridge present, terminating in a small projection at each end of the spore. Two polar capsules spherical. Coiled polar filament not visible in fresh state. Dimensions: diameter  $10\mu$  in average, sutural diameter about  $11\mu$ .

### SPHAEROSPORA ROSTRATA Thélohan

[Fig. 189]

1895    *Sphaerospora rostrata*    Thélohan    1895 : 339

Habitat: Malpighian bodies of kidney of *Mugil* sp.; Roscoff, Le Croisic, Le Vivier-sur-mer, Marseille, Banyuls.

Vegetative form: Not described.

Spore: Subspherical. Shell shows deep longitudinal striations which end in sharp spinous edges at the posterior end. Sutural ridge well marked. Anterior part shows enlargement of quadrangular lamella, which is spinous in side view. Dimensions: 10 to  $12\mu$  in diameter, sutural diameter 1 to  $2\mu$  longer, length of polar filament  $40\mu$ .

Remarks: The parasites cause the degeneration of the Malpighian bodies.

### SPHAEROSPORA MASOVICA Cohn

[Figs. 190 to 192]

1902    *Sphaerospora masovica*    Cohn    1902 : 628-632

Habitat: Gall-bladder of *Abramis brama* L.; Mauersee.

Vegetative form: Polymorphous, due to active movements. Transparent and colorless, while in motion. Endoplasm highly granular, contains yellowish enclosures. Ectoplasm hyaline, forms a narrow layer around the body, occasionally developing into a blunt lobose pseudopodium. Pseudopodia of two kinds; lobose and filose, also intermediate forms. Filiform pseudopodia are formed and retracted more slowly than the lobose. Plasmotomy is of probable occurrence. Two spores are formed in each pansporoblast. Size variable:  $10\mu$  (with no spore),  $18\mu$  (with sporoblasts),  $29\mu$  (with 4 sporoblasts),  $38\mu$  (with 22 sporoblasts). Disporous(?), poly-sporous.

Spore: Spherical. Sutural ridge well marked. Polar capsules and sporoplasm are comparatively small, the former convergent. By warming the spore, polar filament is extruded and at the same time two filaments ("starren Fäden") are made visible at the anterior part of the sutural plane. Sporoplasm with two nuclei, no vacuole being present. Dimensions: diameter  $8\mu$ , length of polar filament  $38\mu$ , length of sutural filament  $14\mu$ .

Remarks: Cohn did not observe free spores in the gall-bladder. He, however, saw many free spores, separated from each other, in the intestine, concluding that the body and pansporoblast membrane of trophozoites, are destroyed in the intestine, setting the spores free.



## SPHAEROSPORA PLATESSAE Woodcock

[Figs. 193 and 194]

1904    *Sphaerospora platessae*    Woodcock    1904 : 59-60

Habitat: Otic-capsule of *Pleuronectes platessa* L.; England.

Vegetative form: Cysts opaque masses about 1mm. in diameter. The cartilage was greatly hypertrophied. Polysporous (presumably).

Spore: Spherical. Shell unornamented. Two polar capsules. Sporoplasm with several refractive granules, but without any vacuole. Dimensions: diameter 8 to 9 $\mu$ , length of polar filament about 70 $\mu$ .

Remarks: Woodcock placed this species provisionally in the genus as he could not examine any fresh material, but had studied smears only.

## SPHAEROSPORA ANGULATA Fujita

[Figs. 195 to 197]

1912    *Sphaerospora angulata*    Fujita    1912 : 261-262

Habitat: Kidney of *Cyprinus carpio* L., *Carassius auratus* L.; Sapporo (Nippon).

Vegetative form: Only description: "The number of the spore in the sporoblast is in this case always less than in the others, rarely exceeding two."

Spore: Somewhat triangular, with convex sides, oval in sideview. Slightly pointed at the mid-posterior margin of the spore. Shell very thin, faintly marked with concentric striations. Two oblong polar capsules are of unequal size. Dimensions: length 7 to 8 $\mu$ , breadth 6 to 7 $\mu$ , thickness 5 $\mu$ , length of largest polar capsule 3.8 $\mu$ , length of polar filament twice as long as that of the spore.

## SPHAEROSPORA POLYMORPHA Davis

[Figs. 198 and 199]

1917    *Sphaerospora polymorpha*    Davis    1917 : 231-232

Habitat: Urinary bladder of *Opsanus tau*; Beaufort (June, July).

Vegetative form: Elongate, but never very irregular in shape. Slowly ameboid. Body colorless. Ectoplasm clearly seen in younger forms, forming one to several large lobate pseudopodia, which in turn extrude several short, conical pseudopodia. In larger forms, ectoplasm is, often, recognizable only at ends of pseudopodia, which in such cases are composed chiefly of endoplasm. Endoplasm granular, vacuolated in some smaller forms, but in larger individuals vacuoles are indistinct or absent; small fat globules abundant in large forms; numbers of rounded sporoblast cells can be distinctly seen. Size of large trophozoites 35 $\mu$  by 50 $\mu$ . Disporous and polysporous (polysporous forms rarely contain many spores at the same time).



the anterior end, one on each side of the sutural plane. Coiled polar filament highly distinct (5 to 6 times) in vivo. Sporoplasm granular, shows two nuclei when stained; no vacuole of any nature. Dimensions in vivo: diameter 8 to 13 $\mu$ , polar capsules 4 to 5 $\mu$  by 2.5 to 3.5 $\mu$ , length of polar filament 35 to 40 $\mu$  (KOH or pressure).

Remarks: No species of the genus, has ever been found in the branchiae. The characters of the spore, however, compel the writer to place the form in the present genus.

### Genus SINUOLINEA Davis

1917	<i>Sinuolinea</i>	Davis	1917 : 219
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The characters of the genus are described on page 57.

Type species: *Sinuolinea dimorpha* Davis.

### SINUOLINEA DIMORPHA Davis

[Figs. 205 to 213]

1916	<i>Sphaerospora dimorpha</i>	Davis	1916 : 333-377
1917	<i>Sinuolinea dimorpha</i>	Davis	1917 : 232-233

Habitat: Urinary bladder and ureter of *Cynoscion regalis*; Beaufort.

Vegetative form: Disporous and polysporous trophozoites differ distinctly from each other. Disporous trophozoites irregular, colorless, transparent and show slow movements. When attached to the epithelium, rounded with one to several pseudopodia. Differentiation of protoplasm distinct. Occasionally endoplasm contains one or more erythrocytes. Average diameter of full-grown form 25 to 30 $\mu$ .

Polysporous form: when attached to the bladder epithelium, the free end is drawn out into a long, cylindrical process, covered with numerous short, hairlike ectoplasmic processes. While not movable, these processes are readily absorbed and reformed. When the trophozoite is detached from the epithelium, the larger end gives rise to numerous conical or arborescent pseudopodia, by means of which the trophozoite moves slowly. Endoplasm extends into the proximal portion of large pseudopodia. It is granular and vacuolated, contains numerous fat globules, refractive granules, yellowish crystals (hematoidin?) and erythrocytes in various stages of disintegration. Endoplasm also contains gemmules, each composed of outer layer and finely granular central portion. Size varies greatly: up to 575 $\mu$  by 90 $\mu$ .

Spore: Spherical. Sutural ridge well marked. Polar capsules large and spherical. Sporoplasm forms a rounded granular mass. Dimensions: diameter 15 $\mu$ , diameter of polar capsules 4.5 $\mu$ , length of polar filament 27 to 35 $\mu$ .

## SINUOLINEA CAPSULARIS Davis

[Figs. 214 to 216]

1917 *Sinuolinea capsularis*

Davis

1917 : 233

Habitat: Urinary bladder of *Paralichthys albiguttus*, *P. dentatus*, *Spheroides maculatus*; Beaufort (July, August).

Vegetative form: Rounded to irregular shape. Body colorless or light yellow. Progressive movements slow. Pseudopodia large branched or arborescent, formed entirely of ectoplasm. Ectoplasm transparent and usually granular, merging gradually with the endoplasm. Endoplasm contains numerous fat globules. In large trophozoites, gemmules are observed. The gemmules are more finely granular and more transparent than the surrounding protoplasm and are practically identical with the small, free trophozoites. Trophozoites containing several gemmules are usually rounded and motionless and appear to be more or less degenerate. Disintegration of such trophozoites were actually observed. Sporulating trophozoites were rare and were never seen to contain gemmules. Size up to  $40\mu$  in diameter. Disporous and polysporous(?).

Spore: Spherical, sometimes slightly elongated. Sutural plane much twisted on its axis. Sutural ridge very distinct. Polar capsules and capsulogenous cells large occupying more than one-half of the cavity of spore. Coiled polar filament distinct. Sporoplasm granular contains numerous fat globules. Dimensions: diameter 12 to  $14\mu$ , diameter of polar capsules  $4.5\mu$ , length of polar filament  $50\mu$ .

## SINUOLINEA ARBORESCENS Davis

[Figs. 217 and 218]

1917 *Sinuolinea arborescens*

Davis

1917 : 233

Habitat: Urinary bladder of *Siphostoma floridae*; Beaufort

Vegetative form: Rounded or irregular. Body colorless or light yellow. Actively ameboid, forming large arborescent pseudopodia of ectoplasm. Ectoplasm well developed, hyaline and homogeneous. Endoplasm coarsely granular, sometimes containing a few fat globules. Larger trophozoites are less active and the ectoplasm less distinct. In sporulating trophozoites the ectoplasm may entirely disappear, the entire trophozoite consisting of a coarsely granular mass. Diameter of rounded sporulating trophozoites  $75\mu$ . Polysporous.

Spore: Rounded, in front view, slightly elongated in the anterior end view. Polar capsules large. Sutural ridge prominent, makes a characteristic S-shaped turn on the anterior end. Coiled polar filaments distinct. Dimensions: length  $15\mu$ , breadth  $12\mu$ , diameter of polar capsules  $5\mu$ .

## SINUOLINEA OPACITA Davis

[Fig. 219]

1917 *Sinuolinea opacita*

Davis

1917 : 234

Habitat: Urinary bladder of *Paralichthys albiguttus*; Beaufort (August).

Vegetative form: Rounded or slightly irregular. Body colorless and opaque. Movements slow. Pseudopodia short lobose. Ectoplasm not distinct, except around ends of pseudopodia, where it forms a thin hyaline layer. Endoplasm opaque, finely granular, with numerous greenish-yellow fat globules varying greatly in size. Diameter of rounded sporulating trophozoites  $22\mu$ , exceptionally large trophozoites  $100\mu$ . Disporous.

Spore: Nearly spherical, with flattened, lateral appendages extending from the posterior side. Sutural plane slightly twisted on its axis. Sutural ridge distinct. Polar capsules large. Coiled polar filament distinct. Sporoplasm finely granular, containing several comparatively large fat globules. Dimensions: diameter 12 to  $13\mu$ , diameter of polar capsules  $4\mu$ .

## SINUOLINEA BRACHIOPHORA Davis

[Fig. 220]

1917 *Sinuolinea brachiophora*

Davis

1917 : 234

Habitat: Urinary bladder of *Paralichthys albiguttus*; Beaufort (August only in one fish).

Vegetative form: Rounded to somewhat irregular. Body colorless. Ectoplasm hyaline. Endoplasm granular, with numerous large fat globules. Disporous.

Spore: Nearly spherical, with a long lateral appendage from each valve. These appendages are empty except at extreme distal end, which contains a granular mass, probably the remains of the parietal cell. Sutural plane slightly oblique to longitudinal axis. Sutural ridge distinct. Polar capsules and capsulogenous cells large, occupying more than half of cavity of spore. Sporoplasm finely granular. Dimensions: length exclusive of appendages 9 to  $11\mu$ , length of appendages 18 to  $22\mu$ , breadth of spore  $9\mu$ , diameter of polar capsules  $3.5\mu$ .

Remarks: Davis mentions that in many respects this species is very similar to *S. opacita*, which occurs in the same host.

## Suborder PLATYSPOREA nom. nov.

The definition of the suborder is recorded on page 57.

## Family MYXIDIIDAE Thélohan

1892	<i>Myxidites</i>	Thélohan	1892 : 173, 175
1893	<i>Myxidiidae</i>	Gurley	1893 : 412

The characters of the family are described on page 57.

## Genus MYXIDIUM Bütschli

1882 *Myxidium*

Bütschli

1882 : Pl. 38

The characters of the genus are described on page 58.

Type species: *Myxidium lieberkühni* Bütschli.

## MYXIDIUM LIEBERKÜHNI Bütschli

[Figs. 221 to 240]

1854		Lieberkühn	1854 : 5-6, 349
1879		Leuckart	1879 : 246
1881		Bütschli	1881 : 638-648
1882	<i>Myxidium lieberkühni</i>	Bütschli	1882 : 593-595
1883		Balbani	1883 : 201-202, 274-275
1891	<i>Myxidium lieberkühni</i>	Pfeiffer	1891 : 20, 91, 105, 127
1894	<i>Myxidium lieberkühni</i>	Gurley	1894 : 283-289
1895	<i>Myxidium lieberkühni</i>	Thélohan	1895 : 340
1895	<i>Myxidium lieberkühni</i>	Cohn	1895 : 5-36
1898	<i>Myxidium lieberkühni</i>	Doflein	1898 : 229, 341
1902	<i>Myxidium lieberkühni</i>	Prenant	1902a : 200-217
1902	<i>Myxidium lieberkühni</i>	Laveran and Mesnil	1902 : 469-472
1906	<i>Myxidium lieberkühni</i>	Léger and Hesse	1906 : 720
1909	<i>Myxidium lieberkühni</i>	Auerbach	1909a : 71
1912	<i>Myxidium lieberkühni</i>	Schröder	1912 : 326-327
1912	<i>Myxidium lieberkühni</i>	Parisi	1912 : 286
1916	<i>Myxidium lieberkühni</i>	Mavor	1916a : 66-68
1916	<i>Myxidium lieberkühni</i>	Mavor	1916b : 373-378

Habitat: Urinary bladder of *Esox lucius* L., *Lota lota* L. (*L. vulgaris*); France, Canada (Georgian Bay), U. S. A., (Wisconsin, Lake Mendota), Italy (Lago Maggiore, Lago di Como, Milano), Germany.

Vegetative form: Form variable with lobose or immovable filiform pseudopodia. Clear differentiation of protoplasm. Cohn described third layer of protoplasm (mesoplasm). Endoplasm yellowish in older trophozoites, contains yellow globules, fat globules and hematoïdin crystals. Size varying with age up to a maximum length of  $300\mu$  by a breadth of  $136\mu$  (Bütschli). Plasmodious multiplication active. Cohn described budding of larger forms, while Laveran et Mesnil observed only the division of smaller forms. Each pansporoblast develops into two spores. Polysporous.

Spore: Elongated fusiform. Shell with longitudinal striations. Polar capsule at each end of the spore. The longer axis of polar capsules coincides with that of spore. Dimensions: length 18 to  $20\mu$ , width 5 to  $6\mu$ . Mavor's measurement: polar capsules  $5\mu$  by 2.5 to  $3\mu$ , length of polar filament 40 to  $45\mu$ .

## MYXIDIUM INCURVATUM Thélohan

[Figs. 241 to 251]

1892	<i>Myxidium ? incurvatum</i>	Thélohan	1892a : 1093-1094
1895	<i>Myxidium incurvatum</i>	Thélohan	1895 : 341
1912	<i>Myxidium incurvatum</i>	Parisi	1912 : 286-287
1912	<i>Myxidium incurvatum</i>	Auerbach	1912 : 4, 39
1916	<i>Myxidium incurvatum</i>	Georgévitch	1916 : 90-91
1917	<i>Myxidium incurvatum</i>	Davis	1917 : 234-235

Habitat: Gall-bladder of *Nerophis aequoreus* L., *N. annulatus*, *N. lumbriciformis*, *Blennius pholis* L., *Callionymus lyra* L., *Fundulus majalis*, *Gambusia affinis*, *Hippocampus brevirostris*, *Mugil cephalus*, *Scorpaena scrofa* L., *Syngnathus acus* L., *S. typhle*; Roscoff, Concarneau, Marseille, Banyuls, Napoli, Bergen, Monaco, Beaufort (July).

Vegetative form: Thélohan describes as follows: Trophozoites usually small, sometimes reaching a considerable size. Pseudopodia lobose. Protoplasm pale and finely granular with refractive globules. Disporous. According to Parisi and Davis rarely monosporous. Georgévitch observed apparently the polysporous form.

Parisi's form: ectoplasm hyaline, endoplasm granular. Monosporous form  $25\mu$  long.

Davis's form: lobose pseudopodia, occasionally being drawn out into a long process. Many trophozoites often cling together closely. Diameter of rounded disporous forms about 13 to  $15\mu$ , that of monosporous forms about 10 to  $11\mu$ .

Spore: Thélohan's description is as follows: Irregular fusiform. Longest axis curved into S-form, both ends sharply pointed and directed toward opposite directions. Polar capsule opening on opposite side of the spore, in some spores the axis of the polar capsules being parallel to each other. Dimensions: length 8 to  $9\mu$ , breadth 4 to  $5\mu$ , length of polar filament 10 to  $15\mu$ .

Parisi gave the following dimensions: length 10 to  $12\mu$ , breadth 5 to  $6\mu$ , length of polar capsule  $3\mu$ , length of polar filament  $28\mu$ .

According to Georgévitch, young spores are not curved (Fig. 245).

Davis's form; Polar filaments when extruded in HCl remained tightly coiled. Dimensions: length 8 to  $9\mu$ , width 5 to  $6\mu$ , diameter of polar capsule about  $3\mu$ .

Remarks: As are shown in figures, Davis's form seems to be somewhat different from the European forms.

## MYXIDIUM SPHAERICUM Thélohan

[Fig. 252]

1895	<i>Myxidium sphericum</i> (corr. <i>sphaericum</i> )	Thélohan	1895 : 341-342
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Habitat: Gall-bladder of *Belone acus* (*Belone belone* L.); Banyuls, Le Vivier-sur-Mer.

Vegetative form: Trophozoites spherical or subspherical, not exceeding 20 to 22 $\mu$  in diameter with lobose pseudopodia formed from the entire surface. Endoplasm granular, contains small refractive granules. Disporous.

Spore: Form similar to *M. incurvatum*, but much greater. Coiled polar filament distinctly visible in fresh spore. Dimensions: length 15 to 20 $\mu$ , width 7 to 8 $\mu$ , length of polar filament 60 $\mu$  (KOH).

## MYXIDIUM HISTOPHILUM Thélohan

[Fig. 253]

1895	<i>Myxidium histophilum</i>	Thélohan	1895 : 341
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Habitat: Connective tissue of kidney and ovary of *Leuciscus phoxinus* L. (*Phoxinus laevis* Ag.); France.

Vegetative form: Small mass.

Spore: Fusiform, being compressed at the middle part. Shell with longitudinal striations. Length of the spore 15 $\mu$ .

## MYXIDIUM sp. Gurley

[Fig. 254]

1851		Leydig	1851 : 226, 234
1852		Leuckart	1852 : 436
1894	<i>Myxidium</i> ? sp. incert.	Gurley	1894 : 290
1899	<i>Myxidium</i> sp.	Labbé	1899 : 92

Habitat: Gall-duct of *Raja batis* L.

Vegetative form: No description.

Spore: Not described. One figure.

## MYXIDIUM DANILEWSKYI Laveran

[Figs. 255 to 257]

1887		Danilewsky	1887 : 35
1897	<i>Myxidium danilewskyi</i>	Laveran	1897 : 725-726
1898	<i>Myxidium danilewskyi</i>	Laveran	1898 : 27-30

Habitat: Kidney of *Emys orbicularis* L.; France.

Vegetative form: Form elongated, circular in cross-section, tapering toward the ends. Body of greenish color, occupying the lumen of the renal tubules of the kidney. Body bent along the cavity of the tubule. Endo-



plasm granular, ectoplasm covering the entire surface of the body as a thin layer. Each pansporoblast develops two spores. Polysporous.

Spore: Elongated fusiform, similar to *M. lieberkühni*, but much smaller. Polar capsule at each end, extrudes filament under the action of nitric acid. Sporoplasm granular with one nucleus. Dimensions: length  $12\mu$ , breadth 3 to  $4\mu$ .

### MYXIDIUM GIGANTEUM Doflein

[Fig. 258]

1898 *Myxidium giganteum*

Doflein

1898 : 285-286

Habitat: Gall-bladder of *Raja asterias*; Napoli.

Vegetative form: Rounded trophozoites. Lobose pseudopodia with slow movement, show remarkable dimensions. Posterior portion forms "Stemm-pseudopodien." Small form club-shaped. Endoplasm is of yellowish color. Diameter of large form  $500\mu$ , of medium sized  $200\mu$ , small individuals  $70-90\mu$ , quite young ones, polymorphous 8 to  $40\mu$ . Larger individual up to  $700\mu$  by  $180\mu$ . Many trophozoites form a cyst-like motionless stage, in which many individuals seem to be covered with a common gelatinous envelope. Each pansporoblast forms two spores. Polysporous.

Spore: Elongated. Fusiform in front view; in side view, one valve arch-form, the other being flat. Transparent. Two polar capsules, one at each end. Coiled polar filament is clearly seen in larger polar capsules. Dimensions: length  $28\mu$ , breadth  $8\mu$ , polar capsules  $8\mu$  by  $4\mu$ .

### MYXIDIUM BARBATULAE Cépède

1906 *Myxidium barbatulae*

Cépède

1906 : 67

1906 *Myxidium barbatulae*

Cépède

1906a : 15-16

Habitat: Kidney of *Cobitis barbatula* L.; Isère.

Vegetative form: Trophozoites form cysts. Form and size vary greatly. Average size: 400 to  $500\mu$  in length and  $200\mu$  in breadth.

Spore: Irregular fusiform. Polar capsule at each end of the spore. Shell longitudinally striated, number being variable. Dimensions: length 12 to  $15\mu$ , breadth about  $6\mu$ , polar capsules  $5\mu$  by 2.5 to  $3\mu$ .

### MYXIDIUM GIARDI Cépède

[Figs. 259 to 261]

1906 *Myxidium giardi*

Cépède

1906a : 16; 1906b : 170-173

1908 *Myxidium giardi*

Cépède

1908 : 93-95

1908 *Myxidium giardi*

Cépède

1908a : 8

Habitat: Kidney of *Anguilla vulgaris* Flem.; Wimereux (August).

Vegetative form: Subspherical white cysts, 800 to  $900\mu$  in diameter, surrounded by a thick (up to  $30\mu$ ) membrane, composed of the connective tissue of the host.

Spore: Irregular fusiform, greatly enlarged at the middle portion. Plane of symmetry of the spore coincides with the sutural plane. Shell thick with 9 to 11 longitudinal striations on each valve, which are more clearly seen on spores stained with iron hematoxylin. Polar capsule at each end. Coiled polar filament distinct. Sporoplasm finely granular with two nuclei and refringent globules. Dimensions *in vivo*: length 9 to 10 $\mu$ , width 5 to 5.6 $\mu$ , thickness 4.75 to 5 $\mu$ , polar capsules 3.5 $\mu$  by 2 $\mu$ .

### MYXIDIUM PFEIFFERI Auerbach

[Figs. 262 to 265]

1908	<i>Myxidium pfeifferi</i>	Auerbach	1908 : 459-464
1910	<i>Myxidium pfeifferi</i>	Auerbach	1910c : 171-172

Habitat: Gall-bladder of *Tinca vulgaris* Cuv.; Karlsruhe.

Vegetative form: Observations in sections. More or less flattened, disc-form, often enrolled. The ectoplasm finely granular, without large pseudopodia. It is not usually distinguishable from the endoplasm which is highly alveolar and contains numerous nuclei, but no enclosures.

Spore: Form varies to some extent. Similar to *Myxidium lieberkühni*; slightly curved. Shell with fine longitudinal striations. Polar capsules two, one at each end. Polar filament is extruded by adding one drop of water to the smear of the spore, which had been dessicated for 24 hours. Sporoplasm with one or two nuclei, in one case with four small nuclei, which is thought to be an abnormal. Dimensions: length 13 to 18 $\mu$ , breadth 5.2 to 5.8 $\mu$ , length of polar capsule 5.2 to 6 $\mu$ , length of polar filament 45 to 54 $\mu$ .

### MYXIDIUM INFLATUM Auerbach

[Fig. 266]

1909	<i>Myxidium inflatum</i>	Auerbach	1909 : 72-74
1909	<i>Myxidium inflatum</i>	Auerbach	1909a : 31
1910	<i>Myxidium inflatum</i>	Auerbach	1910c : 172
1912	<i>Myxidium inflatum</i>	Auerbach	1912 : 39

Habitat: Gall-bladder of *Cyclopterus lumpus* L.; Bergen (September).

Vegetative form: Extremely polymorphous. Rounded, spherical, or much elongated. Ameboid movements very active. Differentiation of protoplasm is sharp and clear, which is best observed in individuals in motion; highly hyaline ectoplasm forms very long lobose pseudopodia, into which granular endoplasm flows in slowly. Size variable. Rounded large form 44 to 45 $\mu$  in diameter. Fully grown spores are set free from the mother trophozoite in comparatively short time. Spore formation similar to that of *Myxidium bergense*. Disporous and polysporous (5 spores in maximum).

Spore: Very broad compared with the length. The longitudinal axis is curved in S shape. Polar capsule situated in opposite way at each end of the spore. Dimensions: length 20.8 to 23.4 $\mu$ , breadth 13 to 15.6 $\mu$ , polar capsules 7.8 $\mu$ , length of polar filament 90 to 100 $\mu$  (KOH).

### MYXIDIUM BERGENSE Auerbach

[Fig. 267]

1908		Keysselitz	1908 : 289
1909	? <i>Myxidium sphaericum</i>	Auerbach	1909 : 75-76
1910	<i>Myxidium bergense</i>	Auerbach	1910 : 61
1910	<i>Myxidium bergense</i>	Auerbach	1910c : 172
1912	<i>Myxidium bergense</i>	Auerbach	1912 : 18-39
1915	<i>Myxidium bergense</i>	Mavor	1915 : 30-31

Habitat: Gall-bladder of *Gadus virens* L., *G. aeglefinis*, *G. merlangus*, *Pleuronectes platessa* and *Sebastes viviparus*, *Melanogrammus aeglefinis*; Norway (Bergen), Canada (St. Andrew, July to September).

Vegetative form: Rounded or elongated, as the result of formation of various pseudopodia. Trophozoites partly free, partly attached to the epithelium of the bladder. Size up to 54 $\mu$  in diameter. Pseudopodia of two kinds: lobose and long filose, sometimes slightly branched. Mavor observed a cyst-like stage under certain conditions, which, he thinks, may be due to some exceptional conditions of the parasite. Plasmogamy. Monosporous, disporous and polysporous.

Spore: Fusiform. Main axis curved into S shape. Form, roughly speaking, very much similar to that of *M. sphaericum* Thél. Dimensions: length 16.2 to 19 $\mu$ , breadth 7 to 9 $\mu$ , length of polar capsules 5.4 $\mu$ , length of polar filament about three times as that of spore.

### MYXIDIUM PROCERUM Auerbach

[Fig. 268]

1910	<i>Myxidium procerum</i>	Auerbach	1910 : 61-62
1910	<i>Myxidium procerum</i>	Auerbach	1910c : 172-173
1912	<i>Myxidium procerum</i>	Auerbach	1912 : 4, 39

Habitat: Gall-bladder of *Argentina silus* As.; Bergen.

Vegetative form: Not observed.

Spore: Greatly elongated and narrow. Sporoplasm with one or two nuclei. Dimensions: length 21.6 to 25.2 $\mu$ , breadth 3.6 to 4 $\mu$ , length of polar capsule 7.2 $\mu$ .

### MYXIDIUM MACKIEI Bosanquet

[Figs. 269 to 271]

1910	<i>Myxidium mackiei</i>	Bosanquet	1910 : 436-438
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Habitat: Renal tubules of kidney of *Trionyx gangeticus*; Bombay. Observations on three slides.

**Vegetative form:** The largest trophozoite  $160\mu$  by  $27\mu$ . No distinction between ectoplasm and endoplasm could be drawn, except in a few individuals in which there was a cyst-wall. Spores are formed in pairs. Protoplasm with two kinds of nuclei, some vesicular, others smaller and compact. Polysporous.

**Spore:** Fusiform with rather pointed ends. Shell finely striated. Two comparatively small polar capsules, one at each end. Sporoplasm with one or two nuclei, contains, often, two large vacuoles. Dimensions: length  $16\mu$  (a few  $17\mu$ ), breadth  $5\mu$  (many broader than this).

**Remarks:** The discoverer, J. P. Mackie mentioned that the parasites did not appear to excite any reaction in the tissue of the host, the animal's health being unaffected.

### MYXIDIUM MACROCAPSULARE Auerbach

[Figs. 272 and 273]

1910    *Myxidium macrocapsulare*    Auerbach    1910 : 440-441

**Habitat:** Gall-bladder of *Scardinius erythrophthalmus* L.; Karlsruhe.

**Vegetative form:** Not observed.

**Spore:** Elongated elliptical when viewed at right angles to sutural plane. Shell somewhat thick with longitudinal striations parallel to the sutural line. In side-view, both ends pointed in diagonally opposite directions. Polar capsules are comparatively large, one at each end, opening at the sharply pointed end. Dimensions: length 10 to  $12\mu$ , breadth  $6\mu$ , polar capsules 3 to  $4\mu$ .

**Remarks:** No pathological change. Bile was clear.

### MYXIDIUM sp. Awerinzew

[Figs. 274 to 276]

1908	<i>Myxidium</i> sp.	Awerinzew	1908 : 33, 43, 45, 55
1909	<i>Myxidium</i> sp.	Awerinzew	1909 : 76, 78, 80, 81
1911	<i>Myxidium</i> sp.	Awerinzew	1911 : 199-204

**Habitat:** Gall-bladder of *Cottus scorpius*; Aleksandrowsk, North Sea.

**Vegetative form:** Trophozoites are small. The protoplasm is differentiated into ectoplasm and endoplasm in some specimens. Very active formation of filiform pseudopodia of various length. Degenerating trophozoites, with one or two empty spaces are often noticed. Each spore is formed independently from each other. Monosporous, disporous and polysporous (with three spores).

**Spore:** Form similar to *Myxidium incurvatum*. Young spores not curved. Dimensions: length 20 to  $35\mu$ , breadth 10 to  $15\mu$ .

## MYXIDIUM DEPRESSUM Parisi

[Figs. 277 and 278]

1912	<i>Myxidium depressum</i>	Parisi	1912 : 287
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Habitat: Gall-bladder of *Citharus linguatula* Gthr.; Napoli (August).  
Vegetative form: Not observed.

Spore: Fusiform with greatly attenuated extremities in front view; flattened and curved in S-form in profile. The axis of polar capsules parallel to each other. Coiled polar filament visible *in vivo*. Sporoplasm with two nuclei, occupies the extracapsular cavity of the spore. Dimensions: length 12 to 14 $\mu$ , breadth 5.5 to 6 $\mu$ , thickness 2.5 to 3 $\mu$ , polar capsules 5.5 to 6 $\mu$  by 2.3 $\mu$ , length of polar filament 30 $\mu$ .

## MYXIDIUM OVIFORME Parisi

[Figs. 279 and 280]

1912	<i>Myxidium oviforme</i>	Parisi	1912 : 287-288
1912	<i>Myxidium oviforme</i>	Auerbach	1912 : 39

Habitat: Gall-bladder of *Apogon rex mullorum* Cuv., *Coris julis* Gthr., *Gadus callarias* L., *Trutta salar* L.; Napoli (August), Norwegian coast.

Vegetative form: Unobserved by Parisi. Auerbach's observation is as follows:

Trophozoites, small ameboid, usually spherical. Size 10 to 12 $\mu$  in diameter. Monosporous (probably).

Spore: Oval with rounded extremities, slightly pointed at the foramina of polar capsules. Shell with numerous fine striations running longitudinally. Polar capsules being often invisible, opening a little above and below of the hypothetical horizontal plane. Sporoplasm fills the extracapsular cavity of the spore, leaving little space at the extremities of the polar capsules. Dimensions: length 11 $\mu$ , breadth 8 to 8.5 $\mu$ , polar capsules 4.5 $\mu$  by 3 $\mu$ , length of polar filament 30 to 35 $\mu$ . Auerbach's measurements: length 12 to 13 $\mu$ , breadth 8 to 9 $\mu$ , polar capsules about 4 $\mu$  long.

## MYXIDIUM ANGUILLAE Ishii

[Figs. 281 to 284]

1915	<i>Myxidium anguillae</i>	Ishii	1915 : 372-382
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Habitat: Integument of the side of the body of *Anguilla japonica* Temm. et Sch.; Schizuoka, Nippon (October). Number of the cysts visible to unaided eye, 10 and 9 on the left and the right side respectively.

Vegetative form: Trophozoites form white and sharply contoured cysts. Cysts, spherical or oval, surrounded by a membranous connective tissue (about 2 $\mu$  thick) of the host. Protoplasm is clearly differentiated into ectoplasm and endoplasm. Diffuse infiltration also occurs. Size measured along the skin, 1.2 to 2mm. in diameter; in sections 1.174mm. by 0.658mm.

Spore: Form similar to *Myxidium pfeifferi* Auerbach, but rather straight fusiform, rarely slightly bent. In many spores the shell tapers to a sharp point at each end. Shell striated longitudinally, 22 in all (2 sutural ridges?). Two polar capsules, one at each end. Sporoplasm usually with two nuclei. Dimensions: length  $9.1\mu$ , breadth  $2.8\mu$ , length of polar capsule  $3.5\mu$ .

MYXIDIUM sp. Mavor

[Figs. 285 and 286]

1915	<i>Myxidium</i> sp.	Mavor	1915 : 32
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Habitat: Gall-bladder of *Pseudopleuronectes americanus*; New Brunswick (Canada), of rare occurrence.

Vegetative form: Observations in smears are as follows: Spheroidal, with numerous long pseudopodia on one side, which suggests the attachment of the trophozoite to the bladder. Trophozoites without any spore. Pansporoblasts spherical, 15 to  $16\mu$  in diameter.

Spore: Spindle shaped. The long axis being slightly bent in S-form. Two pear shaped polar capsules, one at each end of spore. Coiled polar filament visible in fresh state. Dimensions: length 14 to  $15\mu$ , breadth 6 to  $7.5\mu$ , polar capsules  $4\mu$  by  $2.5\mu$ , length of polar filament 90 to  $95\mu$  (ammonia water).

MYXIDIUM GADI Georgévitch

[Figs. 287 to 290]

1916	<i>Myxidium gadi</i>	Georgévitch	1916 : 88-89
1917	<i>Myxidium gadi</i>	Georgévitch	1917c : 797-799
1919	<i>Myxidium gadi</i>	Georgévitch	1919 : 251-289

Habitat: Gall-bladder of *Gadus pollachius*, *Solea vulgaris* Quens; Roscoff (September).

Vegetative form: Highly polymorphous. Spherical or oval. Large forms fill up the bladder. Ectoplasm hyaline and transparent, forming one long or many short lobose pseudopodia. Endoplasm colorless and finely granular, contains more or less large numbers of nucleus. Monosporous, disporous and polysporous.

Spore: Fusiform with attenuated ends. Young spores more attenuated than the fully grown forms. The main axis of the spore coincides with the longitudinal axis of the polar capsules, with slight deviation. Two nuclei of the sporoplasm, are always smaller than those of the shell-valves or of polar capsules. Dimensions: length 6 (?) to  $14\mu$ , breadth 4 to  $6\mu$ .

MYXIDIUM GLUTINOSUM Davis

[Fig. 291]

1917	<i>Myxidium glutinosum</i>	Davis	1917 : 235
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Habitat: Gall-bladder of *Cynoscion regalis*; Beaufort.

**Vegetative form:** Elongated or irregular. Slowly ameboid, moving by means of a broad, lobose pseudopodium of hyaline ectoplasm. Body colorless. Ectoplasm only distinct in pseudopodium. Endoplasm finely granular. The mature spores while still within the mother trophozoites, are surrounded by a clear, refractive gelatinous envelope. Diameter of rounded sporulating trophozoites  $20\mu$ . Disporous.

**Spore:** Cylindrical, ends of valves rounded except at one side, where the polar capsules open at the apex of a small, conical elevation. Spore characterized by the presence of a transparent, homogeneous, gelatinous envelope. Polar capsules pyriform, opening on each side nearly at right angles to the longitudinal axis. Dimensions: length 10 to  $11\mu$ , breadth  $6\mu$ , length of polar capsules  $3\mu$ .

### MYXIDIUM PHYLLIUM Davis

[Figs. 292 and 293]

1917    *Myxidium phyllium*

Davis

1917 : 235

**Habitat:** Gall-bladder of *Gambusia affinis*; Beaufort.

**Vegetative form:** Exceptionally large; flattened, leaflike, usually folded on itself; motionless. Pseudopodia were not observed. Ectoplasm forming a distinct transparent layer around entire body. After being on slide for some time ectoplasm usually becomes covered with very numerous, short, hairlike processes. Endoplasm finely granular, contains numerous fat globules. Diameter up to  $1.35\text{mm}$ . Polysporous.

**Spore:** Fusiform, slightly truncated at each end where polar capsules open. Shell with numerous longitudinal striations. Sporoplasm finely granular, with several small fat globules. Dimensions: length  $11\mu$ , breadth  $8\mu$ , diameter of polar capsules  $3\mu$ .

### MYXIDIUM STRIATUM Cunha et Fonseca

1917    *Myxidium striatum*

Cunha et Fonseca

1917 : 321

**Habitat:** Gall-bladder of *Menticirrhus americanus* L., *Bairdiella ronchus* Cuv. et Val.; Brazil.

**Vegetative form:** More or less spherical. Body small and colorless. Endoplasm granular. Ectoplasm visible when pseudopodia are formed. Pseudopodia filiform, being projected radially. Size variable,  $16\mu$  in diameter in average.

**Spore:** Elliptical. Shell with fine longitudinal striations which run parallel to sutural line. Sutural plane oblique to the longitudinal axis of the spore which is thickened at the extremities. Two ovoidal polar capsules, one at each end. Dimensions: length 10 to  $14\mu$ , breadth 6 to  $8\mu$ , length of polar capsules  $4\mu$ , length of polar filament  $30\mu$ .

## MYXIDIUM KAGAYAMAI nov. spec.

[Figs. 294 and 295]

1916 *Myxidium* sp.

Kudo

1916 : 6

Habitat: Gall-bladder of *Misgurnus anguillicaudatus* Cant.; Tokio (September), 2% of the fish examined infected.

Vegetative form: Not observed.

Spore: Fusiform; one valve being more convex than the other. Suture line straight. Shell with fine longitudinal striations. Dimensions in fixed preparations: length 15 to 18 $\mu$ , breadth 6 to 7 $\mu$ , length of polar capsules 7 to 8 $\mu$ , length of polar filament 60 to 70 $\mu$ .

Remarks: Tho the vegetative form is still unobserved, the author is compelled to consider the present form as a new species by careful reexamination of the material and proposes the name in honor of Dr. T. Kagayama, Tokio, Nippon.

## MYXIDIUM AMERICANUM nov. spec.

[Figs. 622 to 627]

Habitat: In the lumen of urinary tubules of the kidney of *Trionyx spinifera*; Crystal Lake, Urbana, Ill. (July). A single host specimen showed a light infection in the above mentioned organ. No intracellular stage was detected.

Vegetative form: The young trophozoite in the lumen of the tubule of the kidney is multinucleate, and more or less irregular in shape which suggests the ameboid movements of the animal (Figs. 622, 623). The older form with mature spores is rather spherical in form with a distinct outline. The protoplasm is fairly well differentiated into ectoplasm and endoplasm (Fig. 624). The size of the trophozoites varies from 12 to 25 $\mu$  in diameter. A pansporoblast produces two spores. Polysporous.

Spore: Spindle-form; with the two pointed extremities stretched in opposite directions. Circular in cross-section. The shell is rather thin; sutural line is straight. Fine longitudinal striations on the shell, eight to ten in number on each valve. The polar capsules are nearly spherical, coiled polar filament being visible in fresh material (three turns). The polar filament is easily extruded from the fresh spores under the influence of potassium hydrate solution. The direction of the extruded polar filament forms an angle of about 45° with the main axis of the spore and the two filaments are parallel to each other. Preserved spores do not show any filament extrusion under the influence of the said chemical. The sporoplasm is finely granular, and shows, upon staining, two small nuclei of ring-shape, as their peripheral layer takes stain more deeply than the central portion. Average dimensions of fresh spores: length 15 to 16 $\mu$ , breadth 5.5 to 6 $\mu$ , polar capsule 4 $\mu$  by 3.5 $\mu$ , length of polar filament 25 to 32 $\mu$ .



Remarks: Two species of the genus *Myxidium* were reported to occur in chelonian hosts; i.e., *M. danilewskyi* (page 109) and *M. mackiei* (page 112). The former differs from the present form in having an elongated vegetative form which is greenish in color, and in having spores of different shape, dimensions and structure, not to speak of the difference of the host. The latter resembles closely to the species under consideration in dimensions of the spores, but differences in the trophozoite and in the structure of the spore do not allow one to consider two forms as identical. The species is therefore treated as new.

### Genus SPHAEROMYXA Thélohan

1892    *Sphaeromyxa*                      Thélohan                      1892a : 1091-1093

The characters of the genus are described on page 58.

Type species: *Sphaeromyxa balbianii* Thélohan.

### SPHAEROMYXA BALBIANII Thélohan

[Figs. 296 to 307]

1892	<i>Sphaeromyxa balbianii</i>	Thélohan	1892a : 1091-1093
1895	<i>Sphaeromyxa balbianii</i>	Thélohan	1895 : 342
1912	<i>Sphaeromyxa balbianii</i>	Parisi	1912 : 288
1916	<i>Sphaeromyxa balbianii</i>	Georgévitch	1916 : 92-93
1917	<i>Sphaeromyxa balbianii</i>	Davis	1917 : 235-236

Habitat: Gall-bladder of *Motella trcirrata* Bl., *M. maculata* Risso., *Cepola rubescens* L., *Clupea pilchardus*, *Siphostoma floridae*, *S. louisianae*; Roscoff (September), Concarneau, Marseille, Banyuls, Napoli (September), Beaufort (June to August).

Vegetative form: Flattened leaf-like or disc-form, reaching 3 to 4mm. in diameter. Often forms spherical with opaque appearance. The protoplasm is distinctly differentiated into endoplasm and ectoplasm. Ectoplasm forms rounded lobes which exhibit slow movements and show a clear radially striated structure in sections. Endoplasm reticular, contains nuclei, young and mature spores and fat globules. Each pansporoblast develops two spores. Polysporous.

Davis mentions that the largest form he observed was 900 $\mu$  in diameter.

Georgévitch recognized a large number of small trophozoites which were formed by repeated plasmatomous multiplication.

Spore: Fusiform, with truncate ends. Shell longitudinally striated. One polar capsule at each end. Polar filament is wound around an imaginary axis perpendicular to the longitudinal axis of the spore. When extruded, the polar filament is seen as a short, conical and hollow thread-like structure. Sporoplasm finely granular with two nuclei. Dimensions: length 15 $\mu$ , width 5 $\mu$ , length of polar filament 15 $\mu$ .

Parisi gave the following dimensions: length 15 to 20 $\mu$ , width 5 to 6 $\mu$ , polar capsule 7 $\mu$  by 4.7 $\mu$ , length of polar filament 25 to 30 $\mu$ .

Davis' measurements are as follows: length 17 to 20 $\mu$ , breadth 5 to 6 $\mu$ , length of polar filament 20 $\mu$ .

Georgévitch observed young spores with both ends tapering into a point. Later they assume the typical form with truncated ends. He did not recognize the striations on the shell. He also mentions the occurrence of abnormal spores, such as elliptical, spherical forms, etc.; or with only one polar capsule.

### SPHAEROMYXA IMMERSA (Lutz) Thélohan

[Figs. 308 to 311]

1889	<i>Cystodiscus immersus</i>	Lutz	1889 : 84-88
1895	<i>Sphaeromyxa immersa</i>	Thélohan	1895 : 343
1899	<i>Cystodiscus immersus</i>	Lühe	1899 : 291-293

Habitat: Gall-bladder of *Bufo marinus* L. and *Leptodactylus ocellatus* L.; Brazil.

Vegetative form: Leaf-like or disc form, visible thru the bladder wall. Upper and lower sides slightly convex. Size up to 1.5 or 2mm. in diameter; thickness being 1/20 to 1/10 of the diameter. Protoplasm is well differentiated. Ectoplasm transparent and membranous, often contains a large number of micrococcus-like bodies. No ameboid movements nor change of form. Endoplasm highly vacuolar, contains fat globules. Plasmotomic multiplication probably occurs. Spores always arranged in pairs. Polysporous.

Spore: Oval with rounded extremities. Shell more or less thick, with fine transverse striations. Spherical polar capsule at each end. Sutural plane is oblique to the longitudinal axis of the spore. Sporoplasm transparent. Dimensions: length 12 to 14 $\mu$ , breadth 9 to 10 $\mu$ , length of polar filament 50 to 70 $\mu$  (4 to 5 times that of the spore) (KOH).

### SPHAEROMYXA INCURVATA Doflein

[Figs. 312 to 314]

1898	<i>Sphaeromyxa incurvata</i>	Doflein	1898 : 286-287
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Habitat: Gall-bladder of *Blennius ocellatus*; Napoli.

Vegetative form: Trophozoites are found in large masses (Plasmodia ?), in which they form a thin, hollow ball, 5-7mm. in diameter.

As the surface is greater than the inner surface of the bladder, some parts of the body are folded up. Body bluish white and transparent. Protoplasm highly vacuolar, contains numerous fat globules, nuclei and spores. Polysporous.

Spore: Curved to one side along sutural plane and also in a plane at right angles to it. Polar capsule at each end. Sporoplasm with two nuclei.

Polar filament is wound along the longer diameter of the capsule, and relatively thick, but thinner than that of *S. balbianii* Thél. Dimensions: length (along the inner side of the arch) 30 to 35 $\mu$ , breadth 8 $\mu$ , distance between two polar capsules 12 to 15 $\mu$ , polar capsules 12 to 15 $\mu$  by 4 to 5 $\mu$ .

### SPHAEROMYXA SABRAZESI Laveran et Mesnil

[Figs. 315 and 322]

1900	<i>Sphaeromyxa sabrazesi</i>	Laveran et Mesnil	1900 : 380-382
1906	<i>Sphaeromyxa sabrazesi</i>	Schröder	1906 : 455-466
1907	<i>Sphaeromyxa labrazesi*</i>	Schröder	1907 : 359-381
1910	<i>Sphaeromyxa sabrazesi</i>	Schröder	1910 : 1-5
1912	<i>Sphaeromyxa sabrazesi</i>	Parisi	1912 : 288
1913	<i>Sphaeromyxa sabrazesi</i>	Jameson	1913 : 2
1916	<i>Sphaeromyxa sabrazesi</i>	Georgévitch	1916 : 91-92
1916	<i>Sphaeromyxa sabrazesi</i>	Georgévitch	1916a : 3

Habitat: Gall-bladder of *Hippocampus brevis* Cuv., *H. guttulatus* Cuv.; *Syngnathus acus*, *Motella tricirrata*, *Nerophis annulatus*, *Siphonostoma rondeletii*; Arcachon, Rovigno, Napoli, Roscoff (September), Monaco, Villefrance, (March to June).

Vegetative form: Disc form. Diameter up to 2mm. Thickness variable. Body whitish in color. Ectoplasm thin, transparent and homogeneous. Young trophozoites may probably have lobose pseudopodia. Endoplasm highly vacuolated, contains nuclei of various sizes, pansporoblasts, spores and more or less refringent granules. Polysporous.

Schröder observed larger forms up to 5mm. Ectoplasm also was found to project numerous fine short (1 $\mu$ ) hair-like processes from the surface. Each pansporoblast develops into two spores.

Spore: Cylindrical, bent in arch form; with truncated ends. Large cylindrical polar capsule at each end. Sporoplasm granular, contains one nucleus. Polar filament short and conical, is extruded under the action of nitric acid. Dimensions: length 28 $\mu$ , width 4.3 $\mu$ , polar capsule 9 to 10 $\mu$  by 3 $\mu$ , distance between the polar capsules 8 $\mu$ , length of polar filament 8 $\mu$ .

Schröder noticed the stained sporoplasm contained one or two nuclei. He observed indistinctly marked longitudinal striations on the shell. Dimensions: length 22 to 25 $\mu$ , breadth 3 to 4 $\mu$ , polar capsule 8 $\mu$  by 2 to 3 $\mu$ , length of polar filament about 12 $\mu$ .

Georgévitch described the presence of a hyaline substance, containing pale granules, in the spore cavity. Young spores were found to take the form of Myxidium type. In mature spores, he always found two nuclei by staining.

\*Misprinted in Schröder's paper.

## SPHAEROMYXA HELLANDI Auerbach

[Figs. 323 and 324]

1909	<i>Sphaeromyxa hellandi</i>	Auerbach	1909 : 78-79
1910	<i>Sphaeromyxa hellandi</i>	Auerbach	1910b : 772-774
1910	<i>Sphaeromyxa hellandi</i>	Auerbach	1910c : 174-175
1912	<i>Sphaeromyxa hellandi</i>	Auerbach	1912 : 4, 40

Habitat: Gall-bladder of *Molva vulgaris* Flem., *Centronotus gunellus*, *Brosmius brosmie* Asc.; Bergen, Torghattan.

Vegetative form: Large and rounded disc form. Protoplasm is distinctly differentiated into ectoplasm and endoplasm. Thickness up to  $160\mu$ , folded in the bladder. Ectoplasm finely granular; in unstained specimens, it is recognizable as 10 to  $12\mu$  thick layer, in which about  $2\mu$  thick radially striated outer layer and 8 to  $10\mu$  thick inner finely granular region can be distinguished. In stained sections, the outer layer remains unstained. Endoplasm highly alveolar, contains refractive granules of different size which are not stained with Sudan III. Each pansporoblast develops into two spores. Polysporous.

Spore: Arch form in front view. The degree of curvature varies greatly. Sutural line curved in S-shape and well marked. Both ends more or less truncated. Polar capsule at each end. Polar filament being wound along the longest axis of the polar capsule and is extruded with KOH. Sporoplasm rounded with one or two nuclei. Dimensions: length  $20.8$  to  $26\mu$ , breadth and thickness  $5.4\mu$ , length of polar capsule 10 to  $10.8\mu$ .

## SPHAEROMYXA EXNERI Awerinzew

[Figs. 325 and 326]

1913	<i>Sphaeromyxa exneri</i>	Awerinzew	1913a : 155
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Habitat: Gall-bladder of *Thysanophris japonicus*; Lorenzo Marques (Africa).

Vegetative form: Not observed.

Spore: Somewhat resembles that of *S. hellandi* Auer. in being bent to one side with sutural line of S-form but differs in dimensions. Both ends slightly tapering. Polar capsules two, one at each blunt end, in which the polar filament is wound parallel to its longer axis. Sporoplasm comparatively small and sharp-contoured, contains only one nucleus. Dimensions: length 75 to  $80\mu$ , breadth 18 to  $20\mu$ , length of polar capsule 30 to  $35\mu$ .

## SPHAEROMYXA GASTEROSTEI Georgévitch

[Fig. 327]

1916	<i>Sphaeromyxa gasterostei</i>	Georgévitch	1916 : 88
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Habitat: Gall-bladder of *Gasterosteus spinachia*; Roscoff (September).

Vegetative form: Trophozoites form large plasmodia.

Spore: Large, elongated fusiform; ends less truncated than those of the spore of *Sphaeromyxa balbianii*. As the spore becomes mature, the ends assume more pointed shapes. Polar capsules two, one at each end. Sporoplasm with two nuclei, fills the extracapsular cavity. Dimensions: twice or three times larger than those of *Sphaeromyxa balbianii* Thélohan.

Genus ZSCHOKKELLA Auerbach

1910	<i>Zschokkella</i>	Auerbach	1910 : 62-63
			1910a : 240-256
			1910c : 175

The characters of the genus are described on page 58.

Type species: *Zschokkella hildae* Auerbach.

ZSCHOKKELLA HILDAE Auerbach

[Figs. 328 to 331]

1910	<i>Zschokkella hildae</i>	Auerbach	1910 : 62-63
1910	<i>Zschokkella hildae</i>	Auerbach	1910a : 240-254
1912	<i>Zschokkella hildae</i>	Auerbach	1912 : 40-41

Habitat: Urinary bladder of *Phycis blennioides* Br., *Gadus aeglefinis*, *G. callarias* L., *G. virens* L.; Norway.

Vegetative form: Trophozoites float in the bile or attach themselves to the epithelial layer of the bladder. Youngest ameboid form about 4.5 to 6 $\mu$ . In floating form, pseudopodia more or less long, lobose, are formed; while in the attached form those similar to the pseudopodia of *Myxidium bergense* Auer. are developed. Plasmogamy occurs. Size varies greatly according to the number of spores which are formed in each individual. Monosporous (with or without the remnant of protoplasm), disporous and polysporous (up to 4 spores).

Spore: Semicircular in front view, with slightly and equally attenuated ends. At each end, large spherical polar capsule is situated which opens not at the extremity, but on the flat surface. Shell bivalve and thick. Sutural line S-form. Sporoplasm with two nuclei. Dimensions: length 16 to 28.8 $\mu$ , breadth 13 to 18 $\mu$ , polar capsules 5.6 to 7.2 $\mu$  in diameter, length of polar filament 72 $\mu$  (KOH).

ZSCHOKKELLA NOVA Kłokačewa

[Figs. 332 and 333]

1914	<i>Zschokkella nova</i>	Kłokačewa	1914 : 184-186
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Habitat: Gall-bladder of *Carassius vulgaris*; Russia?

Vegetative form: Not observed.

Spore: Outline irregular. Observations on fixed materials alone. Two large round polar capsules open at the side near ends. Sporoplasm with two nuclei. On some spores, striations that run parallel to the sutural line were observed. Dimensions: length 9.5 to 11.5 $\mu$ , breadth 6.5 to 7 $\mu$ , diameter of polar capsule 3 to 3.5 $\mu$ .

## ZSCHOKKELLA ACHEILOGNATHI Kudo

[Figs. 334 to 338]

1916    *Zschokkella acheilognathi*    Kudo    1916 : 3-5

Habitat: Gall-bladder and gall-duct of *Acheilognathus lanceolatum* Temm. et Schl.; Tokio (May). Over 80% of the fish examined were found to be infected.

Vegetative form: Disc-shape. In bile duct, large trophozoites are folded up. Body colorless and transparent. Protoplasm is well defined into two regions. Ectoplasm finely granular *in vivo*. In stained sections, it shows two layers; thin outer layer ( $2\mu$  thick) presents very fine striations, while inner layer (6 to  $8\mu$  thick) is finely vacuolated without any enclosure. Endoplasm is highly vacuolated. Lobose pseudopodia formed only in younger individuals (15 to  $30\mu$  in diameter), in which ameboid movements are not slow. Size: up to  $720\mu$  by  $550\mu$ , thickness 5 to  $30\mu$ . Polysporous.

Spore: Form resembles *Zschokkella hildae*, but slightly elongated. Form varies to some extent. Some spores are of Myxidium type. Sutural line curved. Longitudinally striated. Spherical polar capsule at each end opening near the extremity. Dimensions: length 10 to  $14\mu$ , breadth 6 to  $7\mu$ , diameter of polar capsule 3 to  $5\mu$ , length of polar filament 65 to  $70\mu$  (KOH).

## ZSCHOKKELLA GLOBULOSA Davis

[Figs. 339 and 340]

1917    *Zschokkella globulosa*    Davis    1917 : 236

Habitat: Urinary bladder of *Spheroides maculatus*; Beaufort (August).

Vegetative form: Rounded; slowly ameboid, forming short, lobose pseudopodia. Body colorless and transparent. Ectoplasm not distinct. Protoplasm granular, characterized by the presence of several large fat globules. Sporulating trophozoites about 15 to  $16\mu$  in diameter. Monosporous and disporous.

Spore: Semicircular. Sutural line twisted on its axis and oblique to longitudinal axis; sutural ridge distinct. Polar capsules opening on flat surface. Sporoplasm finely granular and very transparent. Dimensions: length  $11\mu$ , breadth  $7\mu$ , diameter of polar capsules  $3\mu$ .

## Family MYXOSOMATIDAE Poche

1913    *Myxosomatidae*    Poche    1913 : 230

The characters of the family are described on page 58.

## Genus MYXOSOMA Thélohan

1892    *Myxosoma*    Thélohan    1892 : 175

The characters of the genus are described on page 58.

Type species: *Myxosoma dujardini* Thélohan.

## MYXOSOMA DUJARDINI Thélohan

[Figs. 341 to 343]

1841		Müller	1841 : 486-487
1845		Dujardin	1845 : 644
1892	<i>Myxosoma dujardini</i>	Thélohan	1892 : 175
1895	<i>Myxosoma dujardini</i>	Thélohan	1895 : 343-344
1905	<i>Myxosoma dujardini</i>	Nufer	1905 : 77, 79, 186
1910	<i>Myxosoma dujardini</i>	Wegener	1910 : 72-73
1916	? <i>Myxosoma dujardini</i>	Kudo	1916 : 3

Habitat: Branchial lamellae of *Scardinius erythrophthalmus* L., *Perca fluviatilis*, *Leuciscus rutilus* L. and *Cyprinus carpio* L.; France, Frisches Haff, Kurisches Haff (February, April, May), Tokio (May), Switzerland.

Vegetative form: White cysts being branched, rounded, spherical or irregular; 1 to 1.5mm. in diameter.

Wegener's form 1 to 1.7mm. long.

Spore: Ovoidal, flattened, with attenuated anterior end which is slightly bent laterally. Two pyriform polar capsules at the anterior end. Sporoplasm without any iodophilous vacuole. Dimensions: length 12 to 13 $\mu$ , breadth 7 to 8 $\mu$ .

Wegener's form: polar capsules 6 $\mu$  by 3 $\mu$ .

Kudo's form: polar capsules 6 to 7 $\mu$  by 2 $\mu$ , length of polar filament 70 $\mu$ .

## MYXOSOMA (?) LOBATUM Nemeček

[Fig. 348]

1911	<i>Myxosoma</i> (?) <i>lobatum</i>	Nemeček	1911 : 160-162
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Habitat: Branchiae of *Leuciscus leuciscus* L. and *Aspius rapax* Ag.; Austria.

Vegetative form: Cysts spherical, oval or elongated; of white color. Size from 0.5 to 3mm. by 0.5 to 1mm. Those in *Aspius rapax*, oval to spindle-shape, 1 to 3mm. long and 1 to 1.5mm. wide.

Spore: Ovoidal; anterior end narrowly pointed and straight; posterior end rounded, with lobose appendix (about 6 $\mu$  long). A transverse fold on the shell behind the polar capsules in fresh as well as preserved spores. No iodophilous vacuole. Dimensions: length 12.6 $\mu$ , breadth 8.2 $\mu$ , length of polar capsule 4.2 $\mu$ , length of polar filament 80 to 90 $\mu$ . Spores found in *Aspius rapax*, had slight difference in dimensions, the structure, however, being similar to the above.

Remarks: Nemeček doubts if this form is really *Myxosoma* because of the following: 1) different shape of the cysts compared with that of the type species as described by Thélohan; 2) spores observed might develop later into other forms like *Henneguya*.

## MYXOSOMA FUNDULI Kudo

[Figs. 344 to 347]

1918 *Myxosoma funduli*

Kudo

1918 : 12-14

Habitat: Branchiae of *Fundulus majalis* Wal. and *F. heteroclitus* L.; Woods Hole (August, September).

Vegetative form: Cysts. Spherical and small;  $150\mu$  in average diameter. Largest form observed  $360\mu$  by  $264\mu$ . Spores, young and mature, were found in the cysts. Polysporous.

Spore: Pyriform. Shell uniformly thick with 7 to 10 folds on sutural edge at the posterior portion. Sutural ridge, fairly well marked. Two polar capsules pyriform and of equal size at the anterior end. Sporoplasm finely granular with two nuclei but without any iodophilous vacuole. Dimensions: length  $14\mu$ , breadth  $8\mu$ , thickness  $6\mu$ , polar capsule  $8\mu$  by  $2\mu$ , length of polar filament 38 to  $42\mu$  (perhydrol, KOH).

Remarks: The writer could not find any evidence of an iodophilous vacuole by treatment with various iodine mixtures, which is the most important characteristic of the genus. Hahn's form (*Myxobolus funduli*, p. 151) should be distinguished from the present form.

## Genus LENTOSPORA Plehn

1905 *Lentospora*

Plehn

1905 : 150

The characters of the genus are described on page 58.

Type species: *Lentospora cerebralis* (Hofer) Plehn.

## LENTOSPORA CEREBRALIS (Hofer) Plehn

[Figs. 349 to 354]

1903 *Myxobolus cerebralis*

Hofer

1903 : 8

1904 *Myxobolus chondrophagus*

Hofer

1904 : 53

1905 *Lentospora cerebralis*

Plehn

1905 : 145-166

1909 *Lentospora cerebralis*

Plehn

1909 : 38

1910 *Lentospora cerebralis*

Auerbach

1910c : 176

Habitat: Cartilage and perichondrium of *Trutta iridea* Gibb., *Salmo fontinalis* Mitch., *Trutta salar* L.; Germany (Karlsruhe and other localities).

Vegetative form: Ameboid form. Size varies greatly. Small ameboid form probably grows up into large individual which has often fifty or more ringform nuclei and breaks up into numerous small forms by division. No sporous character is observed except a figure of a disporous form.

Spore: Circular in front view; lenticular in side view, with more or less extensive variation in length and breadth. Shell smooth. Sutural ridge distinctly thickened. Two polar capsules pyriform and convergent, are usually of same size. Extruded polar filaments cross each other. Sporoplasm with two ring-form nuclei but without any iodophilous vacuole.



Dimensions: diameter 6 to  $10\mu$ , length of polar capsule  $2/5$  that of the spore, length of polar filament 40 to  $50\mu$  (limewater, 1% KOH).

Remarks: Plehn noticed that the present form causes the chronic form of "Drehkrankheit" among young fish in German waters. She was unable to extrude the polar filament with mineral (?) acids. Auerbach, however, could extrude the filament by means of acids.

#### LENTOSPORA MULTIPLICATA Reuss

[Fig. 355]

1906    *Lentospora multiplicata*    Reuss    1906 : 203

Habitat: Muscle of *Idus melanotus* Heck.; Volga?, Russia.

Vegetative form: Not described.

Spore: Oval. Sutural edge broad with many folds. No iodophilous vacuole. Dimensions: length  $12\mu$ , breadth  $9.5\mu$ , thickness  $6\mu$ , polar capsules  $4\mu$  by  $2.25\mu$ .

#### LENTOSPORA ENCEPHALINA Mulsow

1911    *Lentospora encephalina*    Mulsow    1911 : 483-485

Habitat: In the blood vessel of the brain, especially of the mid-brain of *Cyprinus carpio* L.; Munich (spring). Blood vessels are the only seat of infection. In most cases many individuals lie parallel to one another. The infection occurs frequently and heavily. The effect, however, is undetermined.

Vegetative form: Trophozoite elongated, worm-like and circular in cross section. The body is covered with a pellicula. The protoplasm is distinctly differentiated into homogeneous ectoplasm layer and inner endoplasm. In the latter are found numerous granules, small nuclei and spores.

Spore: Almost circular in front view; profile? No iodophilous vacuole is found. The polar filament is easily extruded by means of a highly diluted KOH solution. Diameter: 5 to  $5.5\mu$ .

#### LENTOSPORA ASYMMETRICA Parisi

[Figs. 356 to 359]

1912    *Lentospora asymmetrica*    Parisi    1912 : 292-293

Habitat: Connective tissue of kidney of *Crenilabrus pavo* C. et V.; Napoli (September).

Vegetative form: One trophozoite found; a small, rounded form with thin and hyaline ectoplasm which could be distinguished from the endoplasm with coarse yellowish globules, containing two spores. Disporous?

Spore: Oval from the front; flattened and fusiform in profile. Sutural edge with many triangular folds, which are more clearly seen in material

preserved in formalin than in fresh condition. Two polar capsules of same size, are situated asymmetrically, opening at the side near the anterior end. Sporoplasm granular and with two nuclei, but without any iodophilous vacuole. The polar filament not being extruded by ordinary reagents, probably because the spores were not full-grown. Dimensions: length 10 to 11 $\mu$ , breadth 6.5 to 7 $\mu$ , length of polar capsules 5 $\mu$ .

### LENTOSPORA ACUTA (Fujita) Kudo

[Figs. 360 to 362]

1912 *Sphaerospora acuta*

Fujita

1912 : 260-261

Habitat: Epithelium of branchial lamellae of *Carassius auratus* L.; Sapporo, Nippon.

Vegetative form: Fujita's description is simply as follows: Sporoblast contains about two spores.

Spore: Spherical in front view, with slightly pointed anterior end; spindle shaped in side-views. Shell thin and smooth. Two convergent polar capsules are of different sizes, occupying about 5/8 in space of the spore. No vacuole could be made out in sporoplasm. Dimensions: length 8 to 10 $\mu$ , breadth 7 to 8 $\mu$ , thickness 5 to 6 $\mu$ , polar capsules 5 $\mu$  by 4 $\mu$ .

Remarks: This species, recorded incompletely by Fujita as *Sphaerospora*, shows characters of the genus *Lentospora* in spore form so that it is provisionally placed here.

### LENTOSPORA DERMATOBIA Ishii

[Figs. 594 to 596]

1916 *Lentospora dermatobia*

Ishii

1916 : 472-474

Habitat: In the integument of *Anguilla japonica* Temm. et Schl.; Shizuoka, Nippon. From the same specimen which harboured *Myxidium anguillae*, see page 114. The number of cysts reaches probably "several hundreds."

Vegetative form: Cysts, beneath the epidermis, usually subcircular, more or less irregularly triangular or quadrilateral under the magnifier, with the largest diameter of from 142 to 267 $\mu$ . The epidermis is slightly lifted up by the cyst. No chromatophore on the surface of the cyst. The cysts separated from each other, are found mostly in the central region of the body, head and fins being free from cysts. In cross-section, cysts exhibit oval or lenticular shape with the longest diameter, which is twice as long as the depth, placed parallel to the surface of the skin. No particular pathological change was noticed.

Spore: Circular in front view; broad fusiform or lenticular in side view. Sutural ridge fairly distinct. Sutural edge comparatively broad, especially

at the posterior margin, where a few folds (three are figured) are seen. Two oval polar capsules convergent and of equal size. Sporoplasm is sharply contoured, no iodophilous vacuole being recognized. Dimensions in preserved material (?): diameter 6.3 to 7 $\mu$ , thickness 4.2 to 4.9 $\mu$ , length of polar capsule 2.8 to 3.5 $\mu$ .

#### Family MYXOBOLIDAE Thélohan

1892	<i>Myxobolides</i>	Thélohan	1892 : 173, 176
1893	<i>Myxobolidae</i>	Gurley	1893 : 412, 413
1895	<i>Myxobolides</i>	Thélohan	1895 : 347

The characters of the family are described on page 58.

#### Genus MYXOBOLUS Bütschli

1882	<i>Myxobolus</i>	Bütschli	1882 : Pl. 38 : 6-10
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The characters of the genus are described on page 58.

Type species: *Myxobolus mülleri* Bütschli.

#### MYXOBOLUS MÜLLERI Bütschli

[Figs. 397 to 403]

1881		Bütschli	1881 : 630
1882	<i>Myxobolus mülleri</i>	Bütschli	1882 : 595
1895	<i>Myxobolus mülleri</i>	Thélohan	1895 : 349
1905	<i>Myxobolus mülleri</i>	Nufer	1905 : 77, 79, 186
1906	<i>Myxobolus mülleri</i>	Cépède	1906 : 64-65
1906	<i>Myxobolus mülleri</i>	Schröder	1906 : 195
1908	<i>Myxobolus mülleri</i>	Auerbach	1908 : 456
1909	<i>Myxobolus mülleri</i>	Auerbach	1909a : 54, 71
1910	<i>Myxobolus mülleri</i>	Wegener	1910 : 81
1911	<i>Myxobolus mülleri</i>	Nemeczek	1911 : 160
1912	<i>Myxobolus mülleri</i>	Parisi	1912 : 293

Habitat: Air bladder and branchiae of *Leuciscus cephalus* L.; kidney and ovary of *L. phoxinus* L.; eye of *Crenilabrus melops* L. and *Alburnus lucidus*; branchiae of *Aspro asper* L., *Barbus vulgaris* Flem., *Leuciscus rutilus* L., *Squalius cephalus* L., *S. agassizii* Heckel, *Lota vulgaris* L., *Phoxinus phoxinus* Ag.; pseudobranchiae of *Cottus gobio* L.; intestine of *Mugil auratus* Risso.; France, Germany [Karlsruhe, Alle (October), Pregel, Frisches Haff], Switzerland (Neuchatel Lake), Italy (Napoli, September).

Vegetative form: White cysts in the connective tissue. Form elongated oval, 2 to 3mm. in diameter. No clear differentiation of protoplasm is observed even in young forms. In sections, some cysts show radiate striations in the thick granule-free ectoplasm. Endoplasm filled with nuclei. Cépède writes as follows: Cysts in branchiae, subspherical or elliptical, 1.5mm. by 0.5mm.

Wegener's form: Cysts small and rounded, 0.2 to 0.3mm. in diameter.

Spore: Ordinarily spherical or subspherical. Two polar capsules

with a small triangular intercapsular appendix. Polar capsules pyriform and of same size. Sutural edge exhibits folds (7 to 9).

Thélohan's dimensions: length 10 to 12 $\mu$ , breadth 9 to 11 $\mu$ , length of polar capsule 5 $\mu$ .

Cépède gave the following dimensions in vivo: length 10 $\mu$ , breadth 9 $\mu$ , thickness 6 $\mu$ , length of polar capsule 5 $\mu$ .

Wegener's form. Usually oval, often almost spherical. Length 10 to 11 $\mu$ , breadth 8 to 9 $\mu$ , diameter of spherical form 9 $\mu$ , polar capsule 4 to 5 $\mu$  by 2 to 3 $\mu$ .

### MYXOBOLUS PIRIFORMIS Thélohan

[Figs. 363 to 364]

1852		Remak	1852 : 144
1883		Balbani	1883 : 197-198
1884		Balbani	1884 : 125
1891		Pfeiffer	1891 : 132
1892	<i>Myxobolus piriformis</i>	Thélohan	1892 : 177
1893	<i>Myxobolus piriformis</i>	Gurley	1893 : 414
1894	<i>Myxobolus piriformis</i>	Gurley	1894 : 211
1895	<i>Myxobolus piriformis</i>	Thélohan	1895 : 348
1905	<i>Myxobolus piriformis</i>	Nufer	1905 : 77, 186
1910	<i>Myxobolus piriformis</i>	Plehn	1910 : 22-27
1910	<i>Myxobolus piriformis</i>	Wegener	1910 : 73

Habitat: Branchiae, spleen, kidney of *Tinca tinca* L., *Cobitis fossilis* L. and subcutaneous connective tissue, spleen, liver, connective tissue of the intestine of *Leuciscus* sp.; France, Germany (Pregel), Switzerland.

Vegetative form: Small, long thread-like cysts. Color white. Polysporous.

Wegener's form: average size, length 1mm., breadth 0.09 to 0.1mm

Spore: Elongated oval; flattened. Anterior end highly attenuated and slightly bent to one side. One pyriform polar capsule at this end. Dimensions: length 16 to 18 $\mu$ , breadth 7 to 8 $\mu$ , length of polar filament 30 $\mu$ .

Wegener gives the following dimensions: length 18 $\mu$ , breadth 7.5 $\mu$ , polar capsule 7.5 $\mu$  by 3.5 $\mu$ .

### MYXOBOLUS UNICAPSULATUS Gurley

[Figs. 365 to 366]

1841		Müller	1841 : 487
1893	<i>Myxobolus unicapsulatus</i>	Gurley	1893 : 414
1894	<i>Myxobolus unicapsulatus</i>	Gurley	1894 : 210-211

Habitat: In the skin of *Labeo niloticus* For.; Nile.

Vegetative form: Cysts very small pustules in the skin of the head.

Spore: Form similar to *Myxosoma dujardini*. A single polar capsule at the anterior end, obliquely directed. Dimensions: length 0.0051''', breadth 0.0034'''.

### MYXOBOLUS FUHRMANNI Auerbach

[Fig. 367]

1909	<i>Myxobolus fuhrmanni</i>	Auerbach	1909 : 65-68
1910	<i>Myxobolus fuhrmanni</i>	Auerbach	1910c : 178-179

Habitat: Connective tissue under the mucous membrane of the mouth of *Leuciscus rutilus* L.; Neuchatel Lake.

Vegetative form: Cysts, of pea-size, surrounded by several membranous layers of connective tissue with a few nuclei. Finely granular ectoplasm forms outer layer. Endoplasm is dense and contains faintly stained nuclei. Pansporoblasts and spores are found in the central portion of the cyst. Polysporous.

Spore: Elongated pyriform, with attenuated anterior and rounded posterior ends. Majority with a single polar capsule; spores with two polar capsules were also observed. Shell thick, at the posterior end. 4 to 6 notch-like markings on the posterior part of the shell. Sutural ridge thickened and fairly well marked. Coiled polar filament visible in preserved material. The opening of the polar capsule is either at the anterior end or near it. Sporoplasm with two nuclei of unequal size and a comparatively large iodophilous vacuole, stained brown with iodine alcohol. Dimensions: length 18 to 20 $\mu$ , breadth about 8 $\mu$ , thickness 6 $\mu$ , length of polar capsule 9 to 10 $\mu$ .

### MYXOBOLUS OCULI-LEUCISCI Trojan

[Fig. 368]

1909	<i>Myxobolus oculi-leucisci</i>	Trojan	1909 : 679-682
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Habitat: Vitreous body of the eye of *Leuciscus rutilus* L.; Prague (May?).

Vegetative form: Two cysts, spherical and subspherical, 100 to 180 $\mu$  in diameter. Ectoplasm finely granular. Outer portion of endoplasm with small nuclei, then larger nuclei each surrounded by protoplasm, while the central portion contains spores. Polysporous.

Spore: Elongated oval, flattened dorso-ventrally. Posterior margin rounded. At the anterior end, a single polar capsule with distinctly visible coiled polar filament. Shell smooth without any markings. Sporoplasm with one nucleus, usually elongated oval (2.8 $\mu$  in diameter) and one vacuole, occupies more than half of the space of the spore. Dimensions: length 9 to 10 $\mu$ , breadth 4.5 to 5.5 $\mu$ , thickness 3 $\mu$ , polar capsule 5 $\mu$  by 2 $\mu$ .

## MYXOBOLUS TOYAMAI Kudo

[Figs. 369 to 370]

1915	<i>Myxobolus toyamai</i>	Kudo	1915 : 517-523
1917	<i>Myxobolus toyamai</i>	Kudo	1917 : 163-170

Habitat:—Connective tissue of branchial lamellae of *Cyprinus carpio* L.; Tokio (July).

Vegetative form: Cysts, ovoidal or in shape of calabash. Small form 67 by 50 $\mu$ , shows clear differentiation of protoplasm. Ectoplasm radially striated, often, differentiates fine processes (2 to 3 $\mu$  long). Endoplasm coarsely granular, contains nuclei from 1 to 4 $\mu$  in diameter. Size up to 190 $\mu$  in greatest diameter in sections. Two spores are formed in each pansporoblast. Polysporous.

Spore: Pyriform, with attenuated anterior and rounded posterior ends. No bilateral symmetry. Lateral sides are curved. Calabash shaped spores often occur. Shell without any marking, thickened at the anterior end. Sutural ridge shows sometimes a short (1.5 $\mu$  long) tail-like process at the posterior tip. A single pyriform polar capsule at the anterior end; in stained preparations, a small, oblong mass of protoplasm is seen between the polar capsule and the shell. Coiled polar filament distinct. Sporoplasm with two nuclei of usually same size and a relatively large iodophilous vacuole, 3 $\mu$  in diameter. Dimensions: length 15 $\mu$ , breadth 7 to 8 $\mu$ , thickness 5 to 6 $\mu$ , polar capsule 7 to 8 $\mu$  by 3 to 4 $\mu$ , length of polar filament 40 to 45 $\mu$  (pressure, perhydrol, KOH).

## MYXOBOLUS NOTATUS Mavor

[Figs. 371 to 372]

1916	<i>Myxobolus notatus</i>	Mavor	1916a : 70-71
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Habitat: Connective tissue of the voluntary muscles on the sides or tail of *Pimephales notatus* Raf.; Georgian Bay, Canada (Summer).

Vegetative form: Cysts as large as 3mm. in diameter, are surrounded by a layer of columnar epithelial cells (origin and significance?) and a dense layer of connective tissue. Protoplasm is not clearly differentiated, tho the cyst is surrounded by an area devoid of nuclei. In the outer region of endoplasm, numerous nuclei each with a caryosome, are recognized. In the course of spore formation, two nuclei for polar capsules appear at first, one of which degenerates later. Polysporous.

Spore: Pyriform, with a posterior extension forming a process, 5 $\mu$  in length and as broad as the spore. A single polar capsule at the anterior end. An iodophilous vacuole in the sporoplasm. Dimensions: length 17 to 18 $\mu$ , breadth 7.5 to 8 $\mu$ , polar capsule 7 $\mu$  by 4 $\mu$ , length of polar filament 95 $\mu$ .

## MYXOBOLUS sp. Kudo

1918 *Myxobolus* sp.

Kudo

1918 : 15

Habitat: Spleen of *Perca flavescens*; West Falmouth, Mass. (August). Isolated spores were noticed in one fish, in smears and section preparations.

Vegetative form: Not observed.

Spore: Ovoidal, attenuated at the anterior end. Shell uniformly thick. A single polar capsule opens at the anterior tip. Sporoplasm contains an iodophilous vacuole and two nuclei of equal size ( $2\mu$ ). Dimensions: length 18 to  $20\mu$ , breadth  $8\mu$ , polar capsule 7 to  $9\mu$  by 3 to  $6\mu$ .

## MYXOBOLUS ROHITAE Southwell et Prashad

[Figs. 373 to 374]

1918 *Myxobolus rohita*

Southwell et Prashad

1918 : 344-347

Habitat: Branchiae of *Labeo rohita*; Turag river, Mirpur, Dacca district, Bengal (June). Type specimens of Indian Museum P48/1. Infection was heavy. In one case 53 cysts were found on one surface of a single gill.

Vegetative form: Cysts in the gill-filaments. The cysts preserved in alcohol are of a creamy-yellow color, oval to cylindrical in form, lying with the long axis parallel to the gill-filaments. Cysts attached to the gill-filaments with the flattened surface. Size: length 3.1 to 3.8mm.; breadth 0.8 to 1.2mm. Cyst-wall striated vertically, covered with an epithelium, two to three layers thick. In the central portion and at the periphery, mature spores and pansporoblasts as well as immature spores were found respectively. Polysporous.

Spore: Elongated pyriform, rounded at the posterior end and acutely pointed anteriorly. Sutural ridge slightly raised. One polar capsule present, being of conspicuous size. Coiled polar filament is distinctly observed in the polar capsule. An iodophilous vacuole,  $3.6\mu$  in diameter, in the sporoplasm. "Lying just posterior to it is the nucleus of the spore. A few granules of chromatin were also seen lying scattered in the protoplasm." Dimensions: length 30 to  $32\mu$ , breadth 7 to  $8\mu$ , length of the polar capsule 22 to  $23\mu$ , that of polar filament 92 to  $97\mu$ .

## MYXOBOLUS SENI Southwell et Prashad

[Figs. 375 to 376]

1918 *Myxobolus seni*

Southwell et Prashad

1918 : 347

Habitat: On the median and caudal fins of *Labeo rohita*; Mirpur, Dacca (January). Type specimens in Indian Museum numbered P 53/1.

Vegetative form: Trophozoites form cysts which are elongated ellipsoidal. Size from 4.7mm. to 5.4mm. in length, 2.9mm. to 3.7mm. in

breadth. Color of the cyst whitish with black scattered granules on the surface.

Spore: Oval, much wider behind than in front and pointed at the anterior end. Sutural ridge is slightly thickened. A single polar capsule, showing much coiled polar filament. Iodinophilous vacuole  $2.3\mu$  in diameter. Dimensions: length 13.2 to  $13.6\mu$ , breadth 10.1 to  $10.3\mu$ , length of polar capsule  $4\mu$ , length of polar filament  $43\mu$  (in one case).

### MYXOBOLUS MISGURNI nov. spec.

[Figs. 377 to 378]

1916    *Myxobolus fuhmanni*    Kudo    1916 : 5

Habitat: Gall-bladder of *Misgurnus anguillicaudatus*; Tokio (September). About 50% of the fish examined showed a few isolated spores floating in the bile.

Vegetative form: Unobserved.

Spore: Form elongated pyriform, with attenuated anterior and rounded posterior ends. Shell uniformly thick. Over sutural edge, shell exhibits many (up to 12) triangular markings. Sutural ridge distinct. A single pyriform polar capsule at the anterior end. Sporoplasm contains an iodophilous vacuole and two nuclei. Coiled polar filament distinct in vivo. Dimensions of fresh spores: length 14 to  $15.5\mu$ , breadth 6 to  $7.3\mu$ , thickness 5 to  $6\mu$ , polar capsule  $6.3\mu$  by 2 to  $3\mu$ , length of polar filament up to  $100\mu$ .

Remarks: The writer reported this species as identical with *Myxobolus fuhmanni* Auerbach. By repeated reexamination and comparison with Auerbach's description, however, he came to the conclusion that the present form should be treated as a new species, on account of the difference of the host and the characters of the spore.

### MYXOBOLUS PFEIFFERI Thélohan

[Figs. 379 to 385]

1890	<i>Myxosporidian</i>	Pfeiffer	1890 : 30-37
1891	<i>Myxosporidian</i>	Pfeiffer	1891 : 100, 105-110, 130
1893	<i>Myxosporidian</i>	Pfeiffer	1893 : 118-130
1895	<i>Myxobolus pfeifferi</i>	Thélohan	1895 : 350
1898	<i>Myxobolus pfeifferi</i>	Doflein	1898 : 306, 320, etc.
1906	<i>Myxobolus pfeifferi</i>	Cépède	1906 : 59
1906	<i>Myxobolus pfeifferi</i>	Stazzi	1906 : 14-19
1906	<i>Myxobolus pfeifferi</i>	Mercier	1906 : 427-428;
			1906a : 763-764
1908	<i>Myxobolus pfeifferi</i>	Keysseltz	1908 : 253-273,
			286-306
1909	<i>Myxobolus pfeifferi</i>	Mercier	1909 : 5-30



**Habitat:** Muscle and connective tissue of kidney, spleen, intestine, ovary, etc., of *Barbus barbus* L., and branchiae of *B. fluviatilis* Ag. and *B. plebejus* Val.; Drac (June), Neckar, Prag, Milano. The cause of well known "Boil disease" (Beulenkrankheit) or Myxoboliasis tuberosa (Hofer) of the barbels in European waters. Among many observers Keysseltz made a thoro study of the parasite. His observations are as follows: The disease occurs among the fish at any stage of growth. About 8% of the fish, 7 to 15cm. long, caught in May and June between Conz and Trier were infected with the parasites. The heaviest infection, however, occurs among fish up to 40cm. in length; fish 50cm. long or larger show the tumors caused by the parasites, rather rarely. Most of the fish die as the result of the infection between the early part of April and the end of October. The highest mortality is reached in the hottest months, i.e., July and August. The temperature greatly affects the growth of the parasites. Fish kept in the aquarium at a temperature of 25° C. or higher demonstrate the growth of the boil in size daily. The boils are not noticed during the winter and spring, they are formed from the early part of April to the middle of October.

**Vegetative form:** The parasites develop tumors of conspicuous size.

Keysseltz's observations are as follows: The tumor varies in size from millet-grains to hen's eggs. Form spherical, oval or elongated. The number of cysts on a single fish, is usually 3 to 4; often one, in some fish, however, 23 were recognized on one fish. Usually tumors separated from each other, rarely many forming one tumor. In one fish, 27cm. in length, a tumor of 7cm. long, 4cm. broad and 3cm. thick, was observed in July. The seat of infection is: the muscle of the body, muscle of pectoral and anal fins, often in peritoneum and rarely in intestine. As the result of breaking up of the cyst membrane, spores are also found in the testis, liver and kidney.

The tumor is composed of many vegetative forms, rounded, oval, elongated, variously branched or flattened. Size reaches to 1.5mm. in diameter. Protoplasm is usually differentiated into ectoplasm and endoplasm. The surface is not often smooth, but shows irregular outline. Ectoplasm is seen often as a very thin, uniformly hyaline, indistinctly granular or radially striated layer, giving the network-like appearance to the surface of the body. Endoplasm, stained more deeply around the peripheral part than other portion, shows a coarsely alveolar structure in the central region. It contains vegetative nuclei, developmental stages of propagative nuclei, granules, fat-like, often leucocytes and red blood corpuscles. The leucocytes, uninuclear or multinuclear, were seen at the periphery, apparently in the course of degeneration. Red blood corpuscles were found, in section, inside of the apparently intact parasite. Each pansporoblast develops into two spores. Polysporous.

Cépède observed one cyst, about 2mm. in diameter, in the connective tissue of the third gill arch.

Spore: Thélohan described as follows: Ovoidal. Sutural edge shows folds. A small triangular intercapsular appendix. Dimensions: length  $12\mu$ , breadth  $10\mu$ . Cépède's form showed exactly the same dimensions.

Keysseltz gave the characters of the spore as follows:

Flattened oval. Shell smooth. A small intercapsular appendix. Sutural edge having a number of small flat enlargement, size and number being variable. Two convergent narrow canals (foramina) penetrate the shell at the anterior end. Two polar capsules, pyriform and of equal or nearly equal size, are located at the anterior half. Coiled polar filament distinct, coiled 7 to 8 times. No distinct connection between polar capsule and the filament. Sporoplasm fills the posterior half of the spore, extending into intercapsular cavity. It is finely reticular, exhibits one or two rounded or oval vesicular nuclei and an iodophilous vacuole. Fat-like substance is often seen around the polar capsules. Spores kept in water for four months remain intact in large numbers. Dimensions: length 12 to  $12.5\mu$ , breadth 10 to  $10.5\mu$ , length of polar capsule, 5.5 to  $6\mu$ , length of polar filament 28 to  $34\mu$ .

#### MYXOBOLUS INAEQUALIS Gurley

[Fig. 411]

1841		Müller	1841 : 487-488
1893	<i>Myxobolus inaequalis</i>	Gurley	1893 : 414
1894	<i>Myxobolus inaequalis</i>	Gurley	1894 : 212

Habitat: In the skin of the head of *Piramutana blochi* Cuv. et Vil. and *Synodontis schall* Bl. Schn.; Guiana, Surinam.

Vegetative form: Very small pustules in the skin of the head.

Spore: Ovoidal. Two polar capsules of unequal size at the anterior end. Dimensions: length 0.0052"', breadth 0.0033'''.

#### MYXOBOLUS DISPAR Thélohan

[Fig. 386]

1895	<i>Myxobolus dispar</i>	Thélohan	1895 : 348
1904	<i>Myxobolus dispar</i>	Hofer	1904 : 50
1910	<i>Myxobolus dispar</i>	Wegener	1910 : 73-74
1911	<i>Myxobolus dispar</i>	Nemeczek	1911 : 145

Habitat: Branchiae of *Carassius carassius* L., branchiae and epithelium of intestine of *Cyprinus carpio* L., also muscle and spleen of *Scardinius erythrophthalmus* L. and in the skin and the connective tissue of *Alburnus lucidus* Heck.; France, Austria, Königsburg (March, July, September).

Vegetative form: Not described by Thélohan.

Wegener's description is as follows: Cysts: white in color; spindle shape with pointed ends. Cysts in *Carassius carassius* L. smaller and oval.

Size 3.5mm. by 0.8mm. Cysts are surrounded by thick layers (7 to 8 $\mu$ ) of the connective tissue of the host. Ectoplasm seems to be undifferentiated. Endoplasm granular, contains a larger number of spores. Polysporous.

Spore: Thélohan's diagnosis is as follows:

Ellipsoidal or slightly oval. Shell with 3 to 5 folds along sutural edge. Polar capsules of unequal size, with a small intercapsular body. The vacuole is difficult to stain with iodine. Dimensions: length 10 to 12 $\mu$ , breadth 8 $\mu$ , polar capsule 7 $\mu$  by 5 $\mu$ .

Wegener's form is as follows: length 11 to 12 $\mu$ , breadth 7.5 to 8 $\mu$ , larger polar capsule 6 to 7 $\mu$  by 3.5 $\mu$ , smaller one 4 $\mu$  by 2.5 to 3 $\mu$ . The sporoplasm is shifted toward the smaller polar capsule.

### MYXOBOLUS ELLIPSOIDES Thélohan

[Figs. 387 to 389]

1852		Remak	1852 : 144-146
1892	<i>Myxobolus ellipsoides</i>	Thélohan	1892 : 177
1895	<i>Myxobolus ellipsoides</i>	Thélohan	1895 : 350-351
1898	<i>Myxobolus ellipsoides</i>	Doflein	1898 : 324, etc.
1905	<i>Myxobolus ellipsoides</i>	Nufer	1905 : 77, 79, 186.
1910	<i>Myxobolus ellipsoides</i>	Wegener	1910 : 74-75
1912	<i>Myxobolus ellipsoides</i>	Lo Giudice	1912 : 1-79

Habitat: Connective tissue of air bladder, branchiae, kidney, spleen, liver and cornea of *Tinca tinca* L., branchiae of *Abramis brama* L., *Alburnus lucidus* Heck., *Leuciscus rutilus* L., *Squalius cephalus* L., *Abramis vimpa* Cuv., *Blicca björkna* L., *Idus melanotus*; France, Vierwaldstätter See, Prague, Masurische See, Italy.

Vegetative form: Thélohan does not describe.

According to Wegener, white cysts, elongated oval; 2mm. by 0.5mm. in size. Polysporous.

Spore: Thélohan described as follows: Flattened elliptical, rather elongated. Sutural edge broad without any folds. Shell with no marking. Form of the spore somewhat variable. Two polar capsules of equal size, capsulogeneous nuclei present even when fully grown. Abnormal spores are of frequent occurrence. Dimensions: length 12 to 14 $\mu$ , breadth 9 to 11 $\mu$ , length of polar capsule 4 $\mu$ .

Wegener's form: length 14 to 15 $\mu$ , breadth 10 to 11 $\mu$ , polar capsule 4 to 5 $\mu$  by 3 $\mu$ . Shell comparatively thick. One spore had a tail 5 $\mu$  long.

### MYXOBOLUS EXIGUUS Thélohan

[Figs. 390 to 395]

1891	<i>Myxosporidium mugilis</i> ?	Perugia	1891 : 23
1895	<i>Myxobolus exiguus</i>	Thélohan	1895 : 349-350
1906	<i>Myxobolus exiguus</i>	Schröder	1906 : 195
1910	<i>Myxobolus exiguus</i>	Wegener	1910 : 75
1912	<i>Myxobolus exiguus</i>	Parisi	1912 : 294-295

**Habitat:** Branchiae of *Abramis brama* L. and *Chondrostoma nasus* L., wall of stomach, pyloric coecum and intestine, branchiae, spleen, kidney of *Mugil chelo* Cuv., *M. capito* Cuv. and *M. auratus* Riss.; Le Vivier-sur-mer, Banyuls, Marseille, Heidelberg, Pregel, Frisches Haff, Kurisches Haff, Geneva, Napoli.

**Vegetative form:** No description by Thélohan.

Wegener writes as follows:

Cysts of variable size. Color white. Usually small and narrow, 0.5 to 0.7mm. long and 0.2mm. wide. Frequently large round cysts of 1.2 to 1.5mm. in diameter, filling the lamella. Cysts are surrounded by 10 to 11 $\mu$  thick membrane composed of the connective tissue of the host. Ectoplasm, 5 $\mu$  thick, is faintly stained by hematoxylin. Outer region of endoplasm, alveolar and densely loaded with nuclei, while in the central portion with mature spores in granular ground-mass.

Parisi's observations are as follows:

Cysts in the intestinal wall of *Mugil auratus*, large; reaching a length of 3mm.

**Spore:** Thélohan's description is as follows:

Flattened ovoidal, with more or less attenuated anterior end. Sutural edge shows fairly noticeable folds. A small triangular intercapsular appendix. Vacuole in the sporoplasm is usually hard to stain with iodine. Dimensions: length 8 to 9 $\mu$ , breadth 6 to 7 $\mu$ , length of polar filament 15 $\mu$  (KOH).

Wegener observed as follows: Rounded with slightly pointed anterior end. Length 8 to 9.5 $\mu$ , breadth 6 to 7.5 $\mu$ , polar capsule 4.5 $\mu$  by 2 to 3 $\mu$ . Shell exhibits small folds around the sporoplasm. An intercapsular triangular body indistinctly visible.

Parisi gave the following dimensions: length 8 to 8.5 $\mu$ , breadth 6 to 7 $\mu$ , thickness 5.5 $\mu$ , polar capsule 3 to 4 $\mu$  by 1.5 to 2 $\mu$ , length of polar filament 30 $\mu$  (alkaline). Folds usually 6 in number. Coiled polar filament visible in vivo.

#### MYXOBOLUS OVIFORMIS Thélohan

[Fig. 396]

1854		Lieberkühn	1854 : 21-22
1892	<i>Myxobolus oviformis</i>	Thélohan	1892 : 177
1895	<i>Myxobolus oviformis</i>	Thélohan	1895 : 351
1905	<i>Myxobolus oviformis</i>	Nufer	1905 : 77, 186
1906	<i>Myxobolus oviformis</i>	Cépède	1906 : 60
1910	<i>Myxobolus oviformis</i>	Wegener	1910 : 76-78

**Habitat:** Fin (subcutaneous tissue), spleen, kidney and liver of *Gobio gobio* L.; branchiae of *Alburnus lucidus* Heck., *Cyprinus carpio* L., *Blicca björkna* L., *Abramis brama* L. and *A. vimba* L.; France (Isère), Frisches Haff (especially spring months), Switzerland.

Vegetative form: Thélohan gave no description.

Wegener's observations are as follows:

Cysts, white, 0.75 to 1.7mm. by 0.4 to 0.7mm. In sections, cysts are shown to be surrounded by a thick (10 to 20 $\mu$ , average 16 $\mu$ ) layer of connective tissue. Ectoplasm a thin (6 to 8 $\mu$  thick) layer, exhibits a transverse striation. The striation is often absent at places in ripe cysts. Endoplasm finely granular. In young cysts, it is, however, reticulated, with nuclei of 1.5 $\mu$  in diameter.

Spore: Thélohan described as follows: Flattened ovoidal with pointed anterior end. Shell smooth. No folds. Polar capsule comparatively large. Dimensions: length 10 to 12 $\mu$ , breadth 9 $\mu$ , polar capsule 6 $\mu$ .

Cépède observed numerous spores in the liver and kidney of *Gobio gobio*. Dimensions in vivo: length 10 to 12 $\mu$ , breadth 9 $\mu$ , length of polar capsule 6 $\mu$ . Polar capsules of equal size. Coiled polar filament distinct.

Wegener's form: length 10.5 to 11 $\mu$ , breadth 7.5 to 8 $\mu$ , polar capsule 5 to 6 $\mu$  by 3 $\mu$ .

Remarks: Wegener recognized another form, which seems to be of very rare occurrence and which can not be distinguished distinctly from the above described form. Cysts at the end of the branchial lamellae. Size 1.7 to 2mm. in largest length. Spore resembles more closely the figure given by Thélohan for *Myxobolus oviformis* than the above mentioned form which he observed. A small intercapsular appendix (rounded) indistinct. Sporoplasm comparatively small. Length 12.5 to 13.5 $\mu$ , breadth 9 $\mu$ , polar capsule 7.5 $\mu$  by 3 $\mu$ .

### MYXOBOLUS LINTONI Gurley

[Figs. 404 to 408]

1891		Linton	1891 : 99-102
1893	<i>Myxobolus lintoni</i>	Gurley	1893 : 414
1894	<i>Myxobolus lintoni</i>	Gurley	1894 : 238

Habitat: Superficial musculature and subcutaneous tissue of *Cyprinodon variegatus*; Woods Hole (August).

Vegetative form: Cysts, not closed, but fungoid masses of an irregular shape, varying in size from 4mm. by 2.5mm. to 10mm. by 4mm., projecting as much as 3mm. above general surface of skin. The skin of the host overlying these tumors, is more or less cracked and broken, the scales being scattered.

Spore: Elliptical in the front view; lenticular in side view. Shell thick. Sutural ridge marked. Two polar capsules, convergent, at the anterior end. Spores kept in alcohol, extruded polar filaments under the action of iodine water and sulphuric acid. Sporoplasm with a large iodophilous vacuole. Dimensions: length 13.9 $\mu$ , breadth 11 $\mu$ , thickness 8 $\mu$ .

## MYXOBOLUS GLOBOSUS Gurley

[Figs. 409 and 410]

1893	<i>Myxobolus globosus</i>	Gurley	1893 : 415
1894	<i>Myxobolus globosus</i>	Gurley	1894 : 241

Habitat: Branchial lamellae of *Erimyzon sucetta oblongus* Lac. (*Catostomus tuberculatus* Le Sueur); Kinston (N.C.), Columbia, (S.C., March), tributaries of Fox River.

Vegetative form: Cysts, whitish, elongated elliptical or rod-shaped, surrounded by very thin membrane? Size up to 0.5mm. in max. length. Polysporous.

Spore: Globose, subcircular in outline. Shell thin and very transparent. Sutural ridge very wide, being one third of the thickness of the spore. Polar capsules two, of equal size, divergent. Vacuole present, but not clearly contoured. Dimensions: length 7 to 8 $\mu$ , breadth 6 to 7 $\mu$ , thickness 5 $\mu$ .

## MYXOBOLUS OBLONGUS Gurley

[Figs. 412 to 416]

1841		Müller	1841 : 487-490
1893	<i>Myxobolus oblongus</i>	Gurley	1893 : 414
1894	<i>Myxobolus oblongus</i>	Gurley	1894 : 234-238

Habitat: Beneath the skin, chiefly of the head of *Erimyzon sucetta oblongus* Lac. (*Catostomus tuberculatus* Le Sueur); Kinston, tributaries of Fox River.

Vegetative form: Cysts, round or elliptic, not over 1mm. in diameter, covered by resistant membrane. Color whitish. Polysporous.

Spore: Spatular, approaching roundish-oblong. Shell thin and transparent. Sutural ridge wide. Two polar capsules, pyriform, of equal size. Sporoplasm extending forward along the upper surface. Vacuole could not be detected. Dimensions: length 14 to 17 $\mu$ , breadth 8.5 $\mu$ , thickness 5 to 6 $\mu$ .

## MYXOBOLUS TRANSOVALIS Gurley

[Figs. 417 and 418]

1893	<i>Myxobolus transovalis</i>	Gurley	1893 : 415
1894	<i>Myxobolus transovalis</i>	Gurley	1894 : 242

Habitat: Under scales on external surface of *Phoxinus* (*Clinostomus*) *funduloides* Girard; 4 Mile Run, Carlisle, Va., tributary of Potomac River (June). No fish of the same species caught from the same locality on August 29 of the same year was found infected.

Vegetative form: It is not certain whether cysts exist or not. Spores in mass, appear to be held together by a small gelatinous or mucoid mass

which has no attachment to the subjacent connective tissue. It forms a thin discoidal mass situated in the center of the concave surface of the scale. The color of the mass slightly more yellowish than the surrounding tissue, when coagulated. It is exceedingly difficult to detect its presence in the fresh state.

Spore: Elliptical, with the largest diameter passing thru two polar capsules. Shell thin. Sutural edge narrow. Two polar capsules of equal size convergent. Polar filament is extruded under the action of glycerine and sulphuric acid. The vacuole in the sporoplasm is difficult to detect. Sporoplasm also contains two nuclei, rarely one, 1 to  $1.5\mu$  in diameter. Dimensions: length 6 to  $7\mu$ , breadth  $8\mu$ .

### MYXOBOLUS OBESUS Gurley

[Figs. 419 and 420]

1883		Balbani	1883 : 203
1893	<i>Myxobolus obesus</i>	Gurley	1893 : 415
1894	<i>Myxobolus ? obesus</i>	Gurley	1894 : 239
1899	<i>Myxobolus obesus</i>	Labbé	1899 : 100
1906	<i>Myxobolus obesus</i>	Cépède	1906 : 60-61

Habitat: On *Alburnus alburnus* L.; branchiae and kidney of *A. lucidus* Heck. (*A. mirandella* Bl.); Lac du Bourget.

Vegetative form: Balbani gave no observation.

Cépède observed as follows: Cysts, ovoidal, more or less elongated or variable in form, not exceeding  $800\mu$  in length. In kidney, numerous cysts were of subspherical, ovoidal or rarely irregularly elongated form. Sub-spherical cysts 500 to  $600\mu$  in average diameter. Polysporous.

Spore: Cépède describes as follows: Subcircular or ovoidal in front view; lenticular in side view. Sutural edge exhibits variable numbers (4 to 5) of fold-like markings on the shell. Polar capsules pyriform and of equal size. Coiled polar filament distinct. A small triangular intercapsular appendix. Sporoplasm with a subspherical and clearly outlined vacuole and two nuclei. Dimensions in vivo: length 11.5 to  $12\mu$ , breadth 7.5 to  $8\mu$ , thickness  $5\mu$ . Those of fixed and stained spores: length 11.25 to  $11.50\mu$ , breadth 7.25 to  $7.50\mu$ , length of polar capsule  $5\mu$ .

Remarks: Cépède mentions that *Alburnus alburnus* L. mentioned by Gurley is "without doubt" identical with *A. lucidus* Heckel.

### MYXOBOLUS CYCLOIDES Gurley

[Fig. 421]

1841		Müller	1841 : 481, 486
1893	<i>Myxobolus cycloides</i>	Gurley	1893 : 415
1894	<i>Myxobolus cycloides</i>	Gurley	1894 : 239
1906	<i>Myxobolus cycloides</i>	Cépède	1906 : 61-63
1910	<i>Myxobolus cycloides</i>	Wegener	1910 : 79-80

Habitat: Opercle, pseudobranchiae and kidney of *Leuciscus rutilus*; branchiae of *Scardinius erythrophthalmus*, *Blicca björkna* L., *Gobio gobio* L., *Abramis vimba* L., *A. brama* L., *Rhodeus amarus* Bl., *Alburnus alburnus* L., *Lota lota* L.; France (Isère), Germany (Pregel, Frisches and Kurisches Haff, Masurische See, January, May).

Vegetative form: Wegener observed cysts as follows. A type: 1 to 2mm. by 0.4 to 0.7mm. Form exactly like that of *Myxobolus oviformis*. B type: small and round, present in groups. C type: small 0.5mm. by 0.2mm.

Spore: Gurley gave the following short diagnosis from the observations of J. Müller: subcircular-ovate or broadly rounded elliptic, length  $12\mu$ .

Cépède distinguishes three different types of spores as follows: Lenticular in side view; subcircular ( $13.5\mu$  by  $13\mu$ ), oval ( $14.7\mu$  by  $11.4\mu$ ) and ovoidal ( $16\mu$  by  $11\mu$ ) in front view. Two polar capsules of equal size ( $6\mu$  by  $4\mu$ ), closely set or separated ( $3\mu$  apart) from each other. Coiled polar filament distinct. A small triangular intercapsular appendix. Sporoplasm refractive and finely granular. Sutural edge exhibits folds of variable number at the posterior portion. Dimensions of fixed and mounted spores: length 10.5 to  $12\mu$ , breadth 7.5 to  $8\mu$ .

Wegener, without noticing Cépède's paper, also mentions three different types chiefly distinguished by the spore as follows:

A type (common form), in the branchiae of *Lota lota*, *Abramis brama*, *A. vimba*, *Blicca björkna*, *Leuciscus rutilus*, *Alburnus alburnus* and *scardinius erythrophthalmus*. Cysts mentioned above.

Spore. Rounded or oval; flattened. A tail,  $15\mu$  long, was noticed twice. A triangular intercapsular appendix. Sutural edge usually having folds. Polar capsules often differ in form and size in different cysts, tho they are constant in one and the same cyst, causing the variability in size of sporoplasm. Dimensions: length 11 to  $12.5\mu$ , breadth 8 to  $9\mu$ , polar capsule  $4.5$  to  $6\mu$  by 3 to  $3.7\mu$ , in many cysts  $7.5\mu$  by  $4\mu$ .

B type. In the fifth gillarch of *Gobio gobio* L. Cysts mentioned above.

Spore. Elongated oval. A triangular intercapsular appendix. Indistinct folds on sutural edge. Dimensions: length 12.5 to  $13.5\mu$ , breadth 8 to  $10\mu$ , polar capsule 5 to  $6\mu$  by 3 to  $4\mu$ .

C type. In the branchiae of *Rhodeus amarus* Bl. and *Alburnus alburnus* L. (April and May). Cysts mentioned above.

Spore. Rounded. Distinct intercapsular appendix. Folds distinct on sutural edge. Dimensions: length 12 to  $15\mu$ , breadth 9 to  $10\mu$ , polar capsule 5 to  $7\mu$  by 3 to  $4\mu$ .

#### MYXOBOLUS SPHAERALIS Gurley

1874		Claparède	1874 : 113-114
1893	<i>Myxobolus sphaeralis</i>	Gurley	1893 : 415
1894	<i>Myxobolus sphaeralis</i>	Gurley	1894 : 240



Habitat: Mucosa of branchiae of *Coregonus lavaretus* L. (*C. fera*); Lake Geneva.

Vegetative form: Cysts, 0.25 to 0.33mm. in diameter. Polysporous.

Spore: Spherical,  $9\mu$  in diameter.

#### MYXOBOLUS ANURUS Cohn

[Figs. 422 and 423]

1895	<i>Myxobolus anurus</i>	Cohn	1895 : 42-43
1896	<i>Myxobolus anurus</i>	Cohn	1896 : 266
1899	<i>Henneguya psorospermica</i>		
	<i>anura</i>	Labbé	1899 : 102
1910	<i>Myxobolus anurus</i>	Wegener	1910 : 76
1911	<i>Henneguya psorospermica</i>		
	<i>anura</i>	Nemeczek	1911 : 146

Habitat: Branchiae of *Esox lucius* L.; Königsberg (March, December), Frisches Haff, Pregel, Masurische See, Lotzen, (September, October).

Vegetative form: Cysts small rounded and of white color. Cohn measures length 0.6mm., breadth 0.34mm. Wegener's form: length 0.3 to 0.5mm. and breadth 0.2 to 0.3mm.

Spore: Cohn's descriptions are as follows: More or less oval. Dimensions: length 12 to  $15\mu$ , breadth 4 to  $6.8\mu$ , polar capsule 5.5 to  $7\mu$  by 2.1 to  $2.5\mu$ , length of polar filament 32 to  $38\mu$ .

Wegener's form: Elongated and narrow, often with a tail. Dimensions: length  $15\mu$  (maximum up to  $18\mu$ ), breadth 6 to  $7\mu$ , polar capsule  $8\mu$  by  $3\mu$ .

Remarks: Tho Labbé classified this as a subspecies of *Henneguya psorospermica* Thélohan, Wegener's observation gives stronger basis for placing this form in the genus *Myxobolus*.

#### MYXOBOLUS sp. Gurley

[Fig. 424]

1882		Bütschli	1882 : 590
1894	<i>Myxobolus</i> sp. incert.	Gurley	1894 : 214
1899	<i>Myxobolus</i> sp.	Labbé	1899 : 100

Habitat: *Nais lacustris* L. (*N. proboscidea*); Locality?

Vegetative form: Cysts, 8mm. by 4.25mm. Polysporous.

Spore: Oval or circular; tailed or untailed. These spores of different form occur, often, without order in the same cyst.

#### MYXOBOLUS sp. Gurley

[Fig. 425]

1894	<i>Myxobolus</i> sp. incert.	Gurley	1894 : 239
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Habitat: Body cavity of *Carassius carassius* L.; Leipsic.

Vegetative form: Not observed.

Spore: Broadly elliptic; shell bivalve; valves equally convex. Sutural ridge. Two equal polar capsules. Sporoplasm with a vacuole. Dimensions: length  $14\mu$ , breadth  $10\mu$ , thickness  $5\mu$ .

Remarks: This species seems to be very similar to *M. carassii* Klokačewa (page 150).

#### MYXOBOLUS sp. Gurley

[Figs. 426 to 429]

1841		Müller	1841 : 480
1894	<i>Myxobolus</i> sp.	Gurley	1894 : 240-241
1899	<i>Myxobolus</i> sp.	Labbé	1899 : 100

Habitat: Skin of opercle, in the branchiae, on the head or on the fin of *Lucioperca lucioperca* L.; Germany, Don.

Vegetative form: Cysts 1.09 to 2.18mm. in diameter. Color whitish. Polysporous.

Spore: Rounded. Thickness equal to half the breadth. Sutural ridge. Two polar capsules, of equal size, converging.

#### MYXOBOLUS CYPRINI Doflein

[Figs. 430 to 432]

1896		Hofer	1896 : 2, 38-39
1898	<i>Myxobolus cyprini</i>	Doflein	1898 : 288, 320, 325
1904	<i>Myxobolus cyprini</i>	Hofer	1904 : 66-67
1909	<i>Myxobolus cyprini</i>	Doflein	1909 : 780-783
1916	<i>Myxobolus cyprini</i>	Doflein	1916 : 1026-1027

Habitat: Suppurative connective tissue and epithelium of kidney, liver and spleen of *Cyprinus carpio* L., rarely *Tinca vulgaris* Cuv. and *Abramis brama* L.; Germany, Austria. According to Hofer the parasites cause so-called "small pox of carp" among carp in German waters.

Vegetative form: Small ameboid. Form irregular. The youngest form with a single or many nuclei, is found in the epithelium of the kidney. Multiplication by multiple division, the nuclei undergoing amitotic division. Endoplasm contains homogeneous, yellow and refractive bodies. Also found in the state of diffuse infiltration. Spores are found in the parenchym of the kidney.

Spore: Oval. Shell thickened ( $1.5\mu$  wide) along the sutural edge. Two converging polar capsules cross each other, in front view, at the anterior tip. Sporoplasm with an iodophilous vacuole. Dimensions: length  $21\mu$ , breadth  $15\mu$ , length of polar capsule  $6\mu$ . Doflein (1916:1027) gives the following dimensions: length 10 to  $16\mu$ , breadth 8 to  $9\mu$ .

Hofer gives the following dimensions: length 10 to  $12\mu$  (up to  $16\mu$ ), breadth 8 to  $11\mu$ , polar capsule 5 to  $6\mu$  by  $3\mu$ , sutural edge  $1.5\mu$ .

## MYXOBOLUS NEUROBIUS Schuberg et Schröder

[Figs. 433 to 436]

1905 *Myxobolus neurobius* Schuberg and Schröder 1905 : 49-56Habitat: Nervous tissue of *Trutta fario* L.; Gutach (May?).

Vegetative form: Cysts, usually elongated, often spherical. Elongated form 0.9mm. by 0.02mm. The seat of the cysts is between the medullary sheath and sheath of Schwann. Neither medullary sheath nor axis-cylinder was infected. Cyst-membrane could not be made out. Cysts contained only full-grown spores without any younger stage. Polysporous.

Spore: Broad oval in front view; spindle shaped in side view. Anterior end attenuated, posterior end rounded. Shell somewhat thick. Sutural ridge is not particularly marked. Edge without any fold. No intercapsular appendix. Sporoplasm, with a large and spherical iodophilous vacuole and a single nucleus, occupies less than one half of the inner space of the spore. Two polar capsules, pyriform, fuse into one at the anterior end. Coiled (8 to 10 times) polar filament distinct. Dimensions: length 10 to 12 $\mu$ , breadth 8 $\mu$ , thickness 6 $\mu$ , polar capsule 6 to 7 $\mu$  by 2 $\mu$ .

## MYXOBOLUS AEGLEFINI Auerbach

[Figs. 437 to 441]

1906	<i>Myxobolus aeglefini</i>	Auerbach	1906 : 568-570
1906	<i>Myxobolus aeglefini</i>	Auerbach	1906a : 115-119
1907	<i>Myxobolus esmarkii</i>	Johnstone and Woodcock	1907 : 204-208
1909	<i>Myxobolus aeglefini</i>	Auerbach	1909 : 76-78
1910	<i>Myxobolus aeglefini</i>	Auerbach	1910c : 181-182
1911	<i>Myxobolus aeglefini</i>	Nemeczek	1911 : 162

Habitat: Cartilage and bone of cranium and eye of *Gadus aeglefinis* G. callarias, *G. merlangus* L., *G. morrhua* L., *G. esmarkii* and *Molva vulgaris* Flem.; Norway, Morecambe (March).

Vegetative form: Cysts in cartilage and bone of cranium and in cartilaginous layer of the sclerotic of the eye. Protoplasm is distinctly differentiated. Ectoplasm somewhat vacuolated; endoplasm granular with numerous small nuclei. Polysporous.

Johnstone's observations are as follows: Round the peripheral part of the cornea, and covered loosely by conjunctiva are a number of milk-white rounded or oval bodies, from about 1 to 3mm. in diameter. Several of these fused to form elongated mass which lie along the curvature of the periphery of the eye. These cysts also invade the lateral and posterior parts of the bulbus oculi. In sections, the cysts lie within the thickness of cartilaginous layer of the sclerotic. This latter is enlarged into thick layer (2mm.) by the presence of the cysts.

Nemeczek mentions irregular cysts of 1.5mm. in diameter.

Spore: Elliptical in front view. Two polar capsules convergent. No intercapsular appendix. Sutural edge rather thick with a number of folds on the posterior margin. Sporoplasm with two nuclei and an iodophilous vacuole. Dimensions: length 10.8 to 11.7 $\mu$ , breadth 9.9 to 10.4 $\mu$ , thickness 7.2 to 9 $\mu$ , length of polar capsule 4.5 to 5 $\mu$ .

Woodcock's form has a spore with the following characters:

Slightly ovoid. Sporoplasm always contains a large and well defined vacuole and two nuclei. Dimensions: length 10 $\mu$ , breadth 8 $\mu$ , length of polar capsule 3.25 to 3.5 $\mu$ .

### MYXOBOLUS GIGAS Auerbach

[Figs. 442 to 445]

1906	<i>Myxobolus gigas</i>	Auerbach	1906 : 386-391
1910	<i>Myxobolus gigas</i>	Auerbach	1910c : 182
1912	<i>Myxobolus gigas</i>	Parisi	1912 : 293-294

Habitat: Subcutaneous connective tissue of the operculum of *Abramis brama* L.; Karlsruhe, Pavia. Parisi observed cysts on the side, on the caudal fin (5 cysts on rays), on other fins, branchiae and in the internal organs of the fish.

Vegetative form: Cysts, spherical or ovoidal. No cyst membrane composed of the connective tissue of the host. Protoplasm is indistinctly differentiated. Ectoplasm thin and radially striated, which gradually turns into endoplasm. Endoplasm finely granular, contains numerous nuclei (2.5 to 2.7 $\mu$  in diameter). Size of greatest form 360 $\mu$  by 290 to 300 $\mu$ . According to Parisi size up to 1.5mm.

Spore: Elliptical when viewed from the front. Sutural edge somewhat narrow, having a number of folds at the posterior portion. Sporoplasm with an iodophilous vacuole and two nuclei. Dimensions: length 16.9 to 21.6 $\mu$ , breadth 13 to 16.2 $\mu$  thickness 9 $\mu$ , length of polar capsules 7.8 $\mu$ , length of polar filament 90 $\mu$  (sulphuric acid).

Parisi gives 150 $\mu$  for the length of polar filament.

### MYXOBOLUS VOLGENSIS Reuss

[Figs. 446 to 448]

1906	<i>Myxobolus volgensis</i>	Reuss	1906 : 200-201
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Habitat: Branchiae, cornea and dorsal fin of *Lucioperca volgensis* Pall; Volga.

Vegetative form: Cysts, spherical, 0.3 to 1mm. in diameter. Polysporous.

Spore: Broad elliptic or rounded. Sutural edge has at least 3 folds. Sporoplasm with an iodophilous vacuole. Dimensions: length 8.25 to 9.5 $\mu$ , breadth 7.25 to 8.25 $\mu$ , thickness 4.5 to 5.5 $\mu$ , polar capsule 3 $\mu$  by 2 $\mu$ .

## MYXOBOLUS SCARDINII Reuss

[Fig. 449]

1906 *Myxobolus scardinii* Reuss 1906 : 201Habitat: Branchiae of *Scardinius erythrophthalmus* L.; Volga.

Vegetative form: Cysts, elongated oval. Smaller cysts rounded oval, 0.8mm. by 0.5mm., the larger forms elongated, 1.2mm. by 0.5mm. Polysporous.

Spore: Broad elliptical. Sutural edge narrow, having folds. A larger triangular intercapsular process. An iodophilous vacuole in sporoplasm. Dimensions: length 11 to 12 $\mu$ , breadth 9 to 9.5 $\mu$ , thickness 4.5 to 5 $\mu$ , polar capsules 5 $\mu$  by 2.5 $\mu$ .

## MYXOBOLUS PHYSOPHILUS Reuss

[Figs. 450 and 451]

1906 *Myxobolus physophilus* Reuss 1906 : 201-202

Habitat: Surface of air bladder of *Scardinius erythrophthalmus* L.; Volga.

Vegetative form: Cysts, rounded, 1.5mm. in diameter. Polysporous.

Spore: Oval, with attenuated anterior end. Sutural edge narrow and smooth. Polar capsules rather large. An iodophilous vacuole in sporoplasm. Dimensions: length 12 to 13 $\mu$ , breadth 8.25 to 9 $\mu$ , thickness 6.5 to 7 $\mu$ , polar capsules 6 $\mu$  by 2.5 $\mu$ .

## MYXOBOLUS MACROCAPSULARIS Reuss

[Fig. 452]

1906 *Myxobolus macrocapsularis* Reuss 1906 : 202Habitat: Branchiae of *Blicca björkna* L.; Volga.

Vegetative form: Cysts, Elongated oval. Size: 1mm. by 0.5mm. Polysporous.

Spore: Oval with greatly attenuated anterior portion. Sutural edge broad and without any fold. Polar capsules rather large. An iodophilous vacuole in sporoplasm. Dimensions: length 11 to 13 $\mu$ , breadth 8.25 to 9.25 $\mu$ , thickness 5.5 $\mu$ , polar capsules 6 $\mu$  by 2.5 to 3 $\mu$ .

## MYXOBOLUS SANDRAE Reuss

[Fig. 453]

1906 *Myxobolus sandrae* Reuss 1906 : 202-203Habitat: Muscle of *Lucioperca sandra* Cuv.; Volga.

Vegetative form: Cysts. Rounded, 0.5mm. in diameter. Polysporous.

Spore: Oval. Sutural edge broad with many distinct folds. An iodophilous vacuole in sporoplasm. Dimensions: length 9.25 to 10 $\mu$ , breadth 7.25 to 8.25 $\mu$ , thickness 4 to 5 $\mu$ , polar capsules 3.5 $\mu$  by 2 $\mu$ .

## MYXOBOLUS BRAMAE Reuss

[Fig. 454]

1906    *Myxobolus bramae*    Reuss    1906 : 203-204Habitat: Branchiae of *Abramis brama* L.; Volga.

Vegetative form: Cysts. Oval, 0.5mm. long, 0.25mm. broad. Polysporous.

Spore: Oval to nearly spherical. Sutural edge narrow and with indistinct folds. Two polar capsules, with a small triangular intercapsular process. An iodophilous vacuole. Dimensions: length 11 to 12 $\mu$ , breadth 9.25 to 10 $\mu$ , thickness 4.5 to 5.5 $\mu$ , polar capsules 4 to 5 $\mu$  by 2.25 $\mu$ .

## MYXOBOLUS CYPRINICOLA Reuss

[Fig. 456]

1906    *Myxobolus cyprinicola*    Reuss    1906 : 204Habitat: Branchiae of *Cyprinus carpio* L.; Volga.

Vegetative form: Cysts, oval, 0.5mm. by 0.3mm. Polysporous.

Spore: Elongated oval. Sutural edge narrow with many indistinct folds. An iodophilous vacuole. Dimensions: length 9.25 to 10 $\mu$ , breadth 7 to 7.25 $\mu$ , thickness 5 to 5.5 $\mu$ , polar capsules 4.5 $\mu$  by 2.5 to 3 $\mu$ .

## MYXOBOLUS BALLERI Reuss

[Fig. 455]

1906    *Myxobolus balleri*    Reuss    1906 : 204-205Habitat: Branchiae of *Abramis ballerus* L.; Volga.

Vegetative form: Cysts. Elongated, 1.5mm. by 0.5mm. Polysporous.

Spore: Oval, slightly pointed at the anterior end. A triangular intercapsular appendix. Sutural edge smooth. An iodophilous vacuole. Dimensions: length 11 to 12 $\mu$ , breadth 9.25 to 10 $\mu$ , thickness 5.5 to 6.5 $\mu$ , polar capsules 5.5 $\mu$  by 2.75 $\mu$ .

## MYXOBOLUS SQUAMAE Keysseltz

[Figs. 457 to 459]

1908    *Myxobolus squamae*    Keysseltz    1908 : 273-274Habitat: Inner surface of the scales of *Barbus fluviatilis* Agass.; Mosel and Neckar.Vegetative form: Form variable; rounded, oval, elongated or rarely branched. The outline of the body is not smooth but irregular with numerous small tooth-like projections with which the body comes in contact with the surrounding substance. The parasites seem to be able to dissolve the substance composing the scale. Length 50 to 800 $\mu$ . In one scale, one or many, up to 8, individuals were found. All showed only advanced stages of spore formation. The parasites are surrounded by a variously developed envelope of connective tissue. Polysporous.

Spore: Elongated oval. Two polar capsules, with 7 to 8 times coiled polar filament. A triangular intercapsular projection. Sporoplasm with an iodophilous vacuole. Dimensions: length 10 to 10.5 $\mu$ , breadth 8 to 8.5 $\mu$ , length of polar capsule 4.5 $\mu$ .

### MYXOBOLUS CORDIS Keysselitz

[Figs. 460 and 461]

1908 *Myxobolus cordis*

Keysselitz

1908 : 279-282

Habitat: Muscle of ventricle, rarely that of bulbus arteriosus of *Barbus fluviatilis* Ag., spores found in kidney, liver and spleen in the condition of somewhat scattered infiltration; Germany (Mosel and Neckar).

Vegetative form: Elongated, oval, sausage or club form. The body whitish, later yellowish. Size from 0.25 up to 4mm., usually 1 to 1.5mm. in length. Propagative stage and cysts observed. One end of the body is held more or less deeply in the muscle and is covered by cellular envelope as in *Myxobolus musculi*, while remaining larger portion of the body is suspended freely inside of the ventricle, covered with a thin layer probably of endocardiac cells. Fish 30 to 45cm. long harboured 40 to 60 parasites. No movements. Ultimately the cysts are formed with differentiated protoplasm. Polysporous.

Spore: Oval. Shell very thin at the anterior end. At the posterior end, cell-like appendage, 2 to 3 $\mu$  wide which is probably formed by both valves, is present. Two pyriform polar capsules at the anterior end, which show the polar filament coiled 7 to 8 times. Sporoplasm with a comparatively large and oval iodophilous vacuole and two nuclei, rarely one (syncaryon). Dimensions: length 12 $\mu$ , breadth 10 $\mu$ , length of polar capsule 4.5 $\mu$ .

### MYXOBOLUS MUSCULI Keysselitz

[Figs. 462 to 464]

1908 *Myxobolus musculi*

Keysselitz

1908 : 282-286

Habitat: Muscle of the main body, rarely that of fins and operculum, and kidney of *Barbus fluviatilis* Agass. of various size (youngest fish found infected, 2 months old), spores in liver, spleen, kidney and ovary (not the ovum) in diffuse infiltration; Mosel and Neckar.

Vegetative form: Elongated. Body whitish opaque, with differentiated protoplasm. Smallest individual observed, 24 $\mu$ . Large form 2mm. in length. Many trophozoites are found closely situated, forming a large mass of parasites that reached dimensions of 4mm. by 2mm. The surrounding envelope, varying in thickness, composed of cells with elongated nuclei as those of perimysium. Young cysts surrounded by thin layer of ectoplasm. Polysporous.

Spore: Oval. Two polar capsules usually unequal. Shell as in *M. cordis* with a small peg closer to the anterior end, polar filament coiled 4 to 5 times, visible in the capsule. Sporoplasm with rarely one (syncaryon), but usually two nuclei and an iodophilous vacuole. A posterior process as is seen in the spores of *M. cordis*, but much smaller, was occasionally observed. Dimensions: length  $11\mu$ , breadth  $8\mu$ , polar capsules  $6\mu$  and  $4\mu$  long.

#### MYXOBOLUS sp. Miyairi

1909 *Myxobolus* sp. Miyairi 1909 : 126

Habitat: Branchiae of loach (*Misgurnus anguillicaudatus* Cant.?); Fukuoka? (Nippon).

Vegetative form: Cysts were not observed.

Spore: No description.

#### MYXOBOLUS sp. Wegener

[Fig. 465]

1910 *Myxobolus* sp. Wegener 1910 : 78

Habitat: Branchiae (gill-arch) of *Perca fluviatilis* L.; Germany (Frisches Haff, March). Only one case.

Vegetative form: Cysts on a gill-arch, white and round, with a diameter of 1.1mm. Polysporous.

Spore: Form and size very variable. Rounded or elliptical, pointed at the anterior end. Sutural edge showing folds at the posterior portion. Dimensions: length 8 to  $10\mu$  (in round form) and  $11\mu$  (in elliptical form), breadth 8 to  $9\mu$ , polar capsules 4 to  $5\mu$  by 2 to  $3\mu$ , length of polar filament  $40\mu$ .

#### MYXOBOLUS PERMAGNUS Wegener

[Fig. 466]

1910 *Myxobolus permagnus* Wegener 1910 : 78-79

Habitat: Branchiae and operculum of *Perca fluviatilis* L., air bladder of *Scardinius erythrophthalmus* L.; Königsberg (May), Pregel (March).

Vegetative form: Cysts rounded in form and white in color, resemble to those of *M. gigas*. No clear ectoplasm layer, nor typical protoplasmic structure. Polysporous.

Spore: Oval, sharply pointed at the anterior end. Sutural edge with 5 to 6 distinct folds at the posterior portion. Polar filament visible in the polar capsules. Dimensions: length 17 to  $18\mu$ , breadth 10 to  $13\mu$ , polar capsules 7 to  $8\mu$  by 3.5 to  $4\mu$ .

#### MYXOBOLUS ROTUNDUS Nemeček

[Fig. 467]

1911 *Myxobolus rotundus* Nemeček 1911 : 156-157

Habitat: Branchiae of *Abramis brama* L.; Austria.



Vegetative form: Cysts, ovoidal or spindle form, 1 to 3mm. long and 1 to 1.5mm. wide. Body white. An extraordinary large number of spores were found in the cysts. Polysporous.

Spore: Round or slightly oval, when viewed from the front. Greatly flattened in side view. Polar capsules convergent, with no intercapsular body. Shell smooth. Sutural edge narrow, without folds. Dimensions: length  $10\mu$ , breadth  $9.8\mu$ , thickness  $3\mu$ , polar capsules 3.8 to  $5\mu$  long, length of polar filament  $40\mu$ .

#### MYXOBOLUS MINUTUS Nemeček

[Fig. 468]

1911 *Myxobolus minutus* Nemeček 1911 : 160

Habitat: Branchiae of *Leuciscus* sp.; Austria.

Vegetative form: Cysts spherical, oval or elongated with white color. Size: 0.5 to 3mm. by 0.5 to 1mm. Polysporous.

Spore: Rounded oval, similar to that of *Myxobolus rotundus*. Shell smooth. Sutural edge narrow without folds. Sporoplasm with an iodophilous vacuole. No intercapsular appendix. Dimensions: length  $6\mu$ , breadth 4.2 to  $5\mu$ , polar capsule  $3\mu$  by  $2\mu$ , length of polar filament 50 to 60, often  $70\mu$ .

#### MYXOBOLUS sp. Lebzelter

1912 *Myxobolus* sp. Lebzelter 1912 : 296-297

Habitat: Gall-bladder of *Thymallus thymallus* L.

Vegetative form: Not observed.

Spore: Sutural ridge distinct. Dimensions, length  $5\mu$ , breadth  $3\mu$ .

#### MYXOBOLUS MAGNUS Awerinzew

[Figs. 469 and 470]

1913 *Myxobolus magnus* Awerinzew 1913 : 75-76

Habitat: Eye of *Acerina cernua* L.; Petrograd.

Vegetative form: Trophozoites form white spots in the tissue of iris, with many spores (300 to 400). Each pansporoblast forms in most cases two, sometimes 3 or 5 spores! Polysporous.

Spores: Large, elongated roundish, slightly flattened. Sutural edge somewhat thick, forming a wide ridge, with 4 to 5 folds at the posterior portion. Polar capsules do not cross each other. Sporoplasm with an iodophilous vacuole and two nuclei. Dimensions: length 38 to  $45\mu$ , breadth 32 to  $38\mu$ , thickness 28 to  $35\mu$ , length of polar capsules 15 to  $17\mu$ , diameter of the vacuole 12 to  $16\mu$ .

#### MYXOBOLUS CARASSII Kłokačewa

[Figs. 471 to 473]

1914 *Myxobolus carassii* Kłokačewa 1914 : 182-184

Habitat: Body cavity, liver and intestine of *Carassius vulgaris* L.; Petrograd?

**Vegetative form:** Cysts spherical. Those in liver and intestine yellowish, surrounded by an envelope composed of fibrous connective tissue. Secondary cysts are formed. Polysporous.

**Spore:** Oval, in front view. Two ovoidal polar capsules convergent at the slightly attenuated anterior end. Coiled polar filament visible. Sporoplasm with an iodophilous vacuole and two nuclei. Sutural edge shows folds in some cases. Dimensions: length 13 to 17 $\mu$ , breadth 8 to 10 $\mu$ , thickness 5 to 7 $\mu$ , polar capsules 6 to 7 $\mu$  long.

**Remarks:** Compare with *Myxobolus* sp. Gurley on page 142.

#### MYXOBOLUS sp. Southwell

1915	<i>Myxobolus</i> sp.	Southwell	1915 : 312-313
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**Habitat:** Subcutaneous intermuscular tissue of *Rasbora* (*Cyprinus*) *daniconius* Day; from a stream near Katwan, Mirzapore (U.P.), India.

**Vegetative form:** 6 cysts found on four fish. The seat is immediately below the scales, in the epidermis. Color milky white. Soft, flattened and roughly oval in shape. Greatest length found, 1.1mm. No pigment was present on the cyst.

**Spore:** Two equal capsules, with a very short tail-like process. Sporoplasm with vacuole; iodine treatment could not be carried out. Dimensions: length 13 $\mu$ , breadth 13 $\mu$ , polar capsule 4 $\mu$  by 4 $\mu$ (?).

**Remarks:** Dimensions, especially that of polar capsule seem to be misprinted. Southwell gave one figure of a fish with a cyst near the dorsal fin. He thinks that "it is quite possible that our parasites may belong to *Myxobolus cyprini*." The incomplete observation without any figure, leads the writer to leave the form also as *Myxobolus* sp. Southwell.

#### MYXOBOLUS FUNDULI Kudo

[Figs. 474 to 476]

1915	<i>Myxobolus musculi</i>	Hahn	1915 : 201-205
1917	<i>Myxobolus musculi</i>	Hahn	1917 : 91-104

**Habitat:** Branchiae and muscle of *Fundulus heteroclitus*, *F. majalis*; Woods Hole. Hahn claims that he succeeded in causing experimental infection in *F. diaphanus* and *Cyprinodon variegatus* by inoculation.

**Vegetative form:** Hahn uses quite a number of different terms from those that are ordinarily used in describing Myxosporidia, without giving any definitions. Naturally it is hard to put what he wrote in several pages in the following lines. Granular vegetative forms produce a great many pansporoblasts, each with a single spore. "Trophoplasm" is difficult to stain. Size: 74 by 33 $\mu$ , 24 by 19 $\mu$ . Cysts within and between the muscle fibers, containing several hundred spores.

**Spore:** Hahn's descriptions may be summarized as follows: Dimensions: length 14.3 $\mu$ , breadth 6.7 $\mu$ , thickness 6.7 $\mu$  to 2/3 of width, polar

capsule,  $6.5\mu$  by  $2\mu$ , polar filament 3 to 4 times the length of the spore ( $42.9$  to  $57.2\mu$ ). Polar filament coiled 10 to 14 times. Shell thin, almost invisible. The spores found in the gill: length  $12$  to  $13.4\mu$ , breadth  $6\mu$  to  $10.4\mu$ . A vacuole is present in the sporoplasm.

Remarks: Examination of Hahn's first paper suggested that he was dealing with the present form as a new species tho he did not mention at all Keysselitz who gave the name *Myxobolus musculi* Keysselitz to the parasite of *Barbus fluviatilis* from German rivers. I was informed by Hahn that he gave the name, *Myxobolus musculi*, without knowing the fact that it was preoccupied by Keysselitz (1908) (see page 148) and that tho he became aware of it later, he can not determine differences by which the two forms can be distinguished. A comparison of the descriptions of Keysselitz and Hahn, however, shows that these two forms differ in several respects. Hence the latter form is recorded here as a distinct species under the new name.

It is interesting to note that very similar forms, one without an iodophilous vacuole at any stage of spore-formation (*Myxosoma funduli* Kudo, see page 125) and the other with a vacuole, occur in the same hosts in the same locality. As mentioned above, the reader is requested to refer to Hahn's original paper for further data.

#### MYXOBOLUS PLEURONECTIDAE Hahn

[Fig. 477]

1917    *Myxobolus pleuronectidae*    Hahn    1917 : 160-161

Habitat: Subcutaneous muscular tissue of *Pseudopleuronectes americanus*; Woods Hole.

Vegetative form: Similar to that of *Myxobolus funduli*.

Spore: Hahn writes as follows: Shape and appearance resembles *Myxobolus pfeifferi*. Dimensions: length  $14.5\mu$ , breadth  $11.9\mu$ , polar capsules  $6\mu$  by  $3.7\mu$ .

#### MYXOBOLUS CAPSULATUS Davis

[Fig. 478]

1917    *Myxobolus capsulatus*    Davis    1917 : 237

Habitat: Visceral connective tissues of *Cyprinodon variegatus*; Beaufort.

Vegetative form: Irregular form. In the state of diffuse infiltration. Polysporous.

Spore: Pyriform, flattened. Polar capsules large and pyriform, filling almost entire cavity of the spore. Sporoplasm relatively small. Iodophilous vacuole visible in living spore. Dimensions: length  $16\mu$ , breadth  $10$  to  $11\mu$ , polar capsules  $11\mu$  by  $4\mu$ , length of polar filament  $84\mu$ .

## MYXOBOLUS NODULARIS Southwell et Prashad

[Figs. 479 and 480]

1918 *Myxobolus nodularis* Southwell and Prashad 1918 : 347

Habitat: In the muscles of *Rasbora daniconius* occurring in two fish on the sides, and in another as a globular cyst near the anus; Mirpur, Dacca (June). Type specimens, numbered P 52/1.

Vegetative form: Cysts rounded or slightly elongated, varying in length 3.5 to 3.8mm. and 2.3 to 2.8mm. in width. Creamy yellow in color, in one case appearing blackish owing to the large number of black granules scattered in its surface.

Spore: Ovoidal. Sutural ridge very wide (about  $\frac{1}{5}$  thickness of the spore). Two polar capsules of equal size, which show coiled polar filaments clearly. Dimensions: length  $9\mu$ , breadth  $7.2\mu$ , length of polar capsule  $3.4\mu$ , that of polar filament  $18.3\mu$ .

## MYXOBOLUS HYLAE Johnston et Bancroft

[Figs. 591 to 593]

1888		Fletcher	1888 : 337
1890		Haswell	1890 : 661
1909	<i>Myxobolus</i> sp.	Johnston	1909 : 29
1910	<i>Myxobolus</i> sp.	Cleland and Johnston	1910 : 25
1918	<i>Myxobolus hylae</i>	Johnston and Bancroft	1918 : 171-175

Habitat: In the testes, vasa efferentia and oviducts of *Hyla aurea*; Sidney, Australia (April, other months not mentioned). Fletcher observed the parasites also in the urinary bladder of both sexes, which fact was not confirmed by Johnston and Bancroft on account of the scarcity of the material. The latter authors could not infect *Hyla caerulea* by feeding infected testes or the cysts, giving the conclusion that the parasite is specific to *H. aurea*. The male is more often attacked by the parasite than the female. The infected animal appeared sickly and emaciated. As to the infection in kidneys, they write as follows: In one male specimen both testes and both kidneys were affected, and the upper parts of the ureters adjacent to the kidneys were swollen and milky in appearance. In another, in addition to the testes, the adjacent kidney and mesentery were attacked. No spores have yet been detected by them in sections of the kidney tubules.

Vegetative form: Johnston and Bancroft describe as follows:

Cysts: in male, either imbedded in the tissue or may project freely into the coelom of the testes; in female, lying between the layers of the wall, being projected into the lumen of the oviduct. Size from those of microscopic dimensions up to 2 to 3mm. in diameter. In sections, the protoplasm

is differentiated into two regions. The outer layer (ectoplasm) surrounds the body as a thin, light-staining region, while the endoplasm being denser and of more or less granular structure filled with spores especially in the central portion.

Spore: Johnston and Bancroft describe as follows:

Form somewhat variable, caused by the reduction in length. Oval, egg-shaped or nearly circular in front view. Sutural ridge slightly thickened. Two pyriform polar capsules are located at the anterior end. Sporoplasm with an iodophilous vacuole ( $2\mu$  in diameter), shows usually two distinct nuclei, rarely but one. Dimensions: length variable, diameter of circular form 7 to  $8\mu$ , breadth 8 to  $10\mu$ , thickness about  $6\mu$ , thickness of shell  $1\mu$ , polar capsules 4 to  $5\mu$  by  $2\mu$ , length of polar filament 90 to  $98\mu$  (acids or alkalies).

### MYXOBOLUS AUREATUS Ward

[Figs. 643 to 649]

1919     *Myxobolus aureatus*

Ward

1919 : 49

Habitat: Between the ectodermal layers of the fin membrane of *Notropis anogenus*; Put-in-Bay, Lake Erie (August). Out of thirty fish, two to three cm. in length, seven were found to be infected. The infected fish were not inferior in size or vigor to others of the same species. The most heavily infected one was the most vigorous of all. The number of cysts in the individual fish, varied from one to forty, being confined in the fin. The cysts are always separated from each other, tho in a few instances they were apparently connected.

Vegetative form: The parasite forms cysts between the ectodermal layers of the fin membrane. The cyst is a smooth margined ellipsoid, measuring from 1 to 1.6 mm. in layer diameter and from 0.8 to 1.2 mm. along its transverse axis. The opaque cyst is of a clear orange yellowish color. This gilt color is contained in the cyst wall, fading away in alcohol and formol. The chromatophores of the skin of the host are distinctly more abundant on the cyst than in other parts of the skin, and the older the cyst the more abundant the chromatophores. The wall of the cyst is noticeably tough and thick. In section, the protoplasm shows a poor differentiation into ectoplasm and endoplasm. The former granular and reticular, covers the entire surface as a thin layer, while the latter is highly vacuolated, containing only mature spores. Polysporous.

Spore: Ovoid; slightly pointed anterior and rounded posterior ends in front view; slightly compressed in lateral view. Sutural ridge distinct. The shell is of moderate thickness, and bears a flange at the posterior half in some spores. Two pyriform polar capsules, frequently of slightly different dimensions, are at the anterior part of the spore. No intercapsular appendix is present. When the spore is allowed to stand for 24 hours

or more in water, the polar filaments are extruded. The binucleated finely granular sporoplasm shows an iodophilous vacuole. Dimensions: length 12.4 to 13.5 $\mu$ , breadth 6.5 to 7.5 $\mu$ , thickness 5 $\mu$ , length of polar capsule 6 to 7 $\mu$  (rarely 7.5 $\mu$ ), length of polar filament about 20 to 26 $\mu$ , diameter of iodophilous vacuole about 2 $\mu$ .

MYXOBOLUS MIYAIRII nov. spec.

[Fig. 481]

1909 *Myxobolus* sp.

Miyairi

1909 : 130, 131-132

Habitat: Intestinal wall of *Parasilurus asotus* L.; Fukuoka ? (Nippon)

Vegetative form: Cysts. Size rather small up to 0.5mm. Full-grown spores as well as those in developmental stages fill the central portion of cysts, while numerous nuclei are chiefly found along the periphery of endoplasm.

Spore: Elongated elliptic. Two polar capsules of nearly same size. Sporoplasm with a comparatively large iodophilous vacuole. Dimensions: length 13 to 14.5 $\mu$ , breadth 6 to 7 $\mu$ , length of polar capsules 4.5 $\mu$ , length of polar filament 30 to 35 $\mu$ .

Remarks. As the descriptions show the form and structure are distinguishable from other species, the writer establishes the present species.

MYXOBOLUS KOI nov. spec.

[Figs. 482 to 485]

Habitat: In the connective tissue of the gill filament of *Cyprinus carpio* L.; Tokio (April). One fish was found infected in a slight degree.

Vegetative form: Cysts small and spherical; white in color. Size up to 230 $\mu$  in largest diameter. The seat similar to *Myxobolus toyamai*. The structure of the cysts, observed in section preparations, is also similar to the above mentioned unicapsular *Myxobolus*.

Spore: Oval with attenuated anterior and rounded posterior ends in front view; elongated pyriform in side view. Shell comparatively thin. No marking on shell. Sutural ridge fairly well marked. No intercapsular appendix. Two polar capsules are pyriform, large, and of usually equal form and size. Coiled polar filament distinct in vivo. Sporoplasm rather small, finely granular, shows two nuclei in almost all spores. An iodophilous vacuole is deeply stained by Lugol's solution. Dimensions: 14 to 16 $\mu$ , breadth 8 to 9 $\mu$ , thickness 5 to 6 $\mu$ , polar capsule 8 to 9 $\mu$  by 2.5 to 3 $\mu$ , length of polar filament 72 $\mu$  in average (KOH).

MYXOBOLUS ORBICULATUS nov. spec.

[Figs. 566 to 576]

Habitat: Muscle of myotomes of *Notropis gilberti* J. et M.; Stony Creek, Ill. (November). The fish was kept alive in an aquarium from November

11, 1918, until March 10, 1919, when it was killed, being then nearly dead. The material was examined on March 15. A few isolated spores occurred in the muscle of *Notropis blennioides* (Homer Park, Ill., November).

**Vegetative form:** In and between the muscle bundles of the myotomes. Size variable. Color opaque white under the dissecting microscope. Smallest rounded ameboid forms with a single or numerous nuclei, in the muscle bundle, have the size of from  $10\mu$  to  $30\mu$  in greatest diameter (Figs. 573 to 575). The largest form observed was  $400\mu$  by  $120\mu$ . Young forms without any differentiated protoplasm, shows indistinct granular and reticular structure with deeply staining spherical or ring-form chromatinic granules. The number of the nuclei increases with the growth of the body. Larger form (Fig. 576), spindle shape, circular in cross-section, lies with its long axis parallel to the muscle fibres. The protoplasm vacuolated, contained mostly mature spores. Spores were also found in the state of diffuse infiltration. Polysporous.

**Spore:** Form somewhat variable. Typical form almost circular, slightly pointed at the anterior end (Fig. 566) in front view; spindle shaped in profile (Figs. 569 and 570). Sutural ridge marked. Shell uniformly thick, usually exhibiting four triangular folds on the surface along the posterior margin (Figs. 566, 568 and 571). No intercapsular appendix. Two pyriform polar capsules are, as a rule, of the same size and form. Frequent occurrence of the inequality of the polar capsules together with abnormalities in the form of the spore, were noticed especially among comparatively young spores. The granular sporoplasm, shows two spherical nuclei when stained. The iodophilous vacuole, spherical and  $2\mu$  in average diameter, is deeply stained with Lugol's solution. Dimensions of unstained preserved spores: length and breadth 9 to  $10\mu$ , thickness  $6.5$  to  $7\mu$ , polar capsule 6 to  $7.5\mu$  by  $2.5$  to  $3\mu$ .

#### MYXOBOLUS DISCREPANS nov. spec.

[Figs. 597 to 601]

**Habitat:** Branchial lamellae of *Carpiodes diffinis*; Salt Fork, Urbana, U.S.A. (May). One fish caught, died (soon after the capture) two hours before being fixed. Length 8.5cm.

**Vegetative form:** The parasites formed numerous cysts on the branchial lamellae. Cysts slightly yellowish white and mostly rounded or elongated along the lamella, occur in groups, often occupying the entire lamella. Infection was fairly heavy. Every gill arch harbored ten to twenty cysts mostly on the outer surface. Size of the cyst varies, small rounded one  $500\mu$  in diameter up to elongated forms 2mm. by 0.5mm., the majority being from 0.5 to 1mm. in diameter. The cyst is surrounded by a thin connective tissue layer of the host. The protoplasm shows little differen-

tiation. The ectoplasm is a rather narrow zone around the entire body and the endoplasm is filled with various nuclei, several stages of developing pansporoblasts, and mature spores. Each pansporoblast produces two spores. Polysporous.

Spore: Approximately circular with broad anterior and more or less narrower posterior end in front view; broadly fusiform in profile. Shell uniformly thin with 5 to 6 markings on the posterior margin. Two polar capsules broadly oval and convergent, fill the anterior half of the spore. A small triangular intercapsular appendix presents. Coiled polar filament is fairly visible in vivo. The spores from the cysts which were fixed with alcohol-acetic and preserved in 95 per cent alcohol, showed the extrusion of the polar filament under the influence of potassium hydrate solution (35 per cent) even after a considerable length of time as is shown in the following:

Material fixed on May 29.

June 2; Extrusion took place in almost all spores.

June 10; Extrusion took place in almost all spores.

June 26; Extrusion took place in almost all spores.

July 28; Extrusion took place in almost all spores.

August 29; Extrusion took place in numerous spores.

September 29; Extrusion took place in about 70 per cent of the spores, some filaments being rather short, and not fully extended.

October 20; Extrusion took place in about 50 per cent of the spores, most filaments being short, and not fully extended.

Sporoplasm coarsely granular shows clearly two ring-form nuclei in fresh preparations. Dimensions of preserved spores: length 11.4 to 13.5 $\mu$ , breadth 9.5 to 11 $\mu$ , thickness 8.5 to 9.5 $\mu$ , polar capsule 5.5 to 6 $\mu$  by 3.5 to 4 $\mu$ , length of polar filament 50 to 55 $\mu$ .

Remarks: The present species differs from the hitherto known species. *Myxobolus lintoni* (page 138) and *Myxobolus orbiculatus* (page 155) which are the nearest to the present form, differ from *Myxobolus discrepans* in the host, organ of infection, vegetative form and form and structure of the spore.

#### MYXOBOLUS MESENTERICUS nov. spec.

[Figs. 628 to 631]

Habitat: In the mesentery, liver, spleen and wall of stomach, pyloric coecum, intestine, and gall-bladder of *Lepomis cyanellus*; Crystal Lake, Urbana, Ill. (June and July). Out of thirty-six host fish, 10 cm. in average length, seven were found to be infected. In every case, except one, the mesentery was the main seat of infection, harboring conspicuous cysts. The number of cysts found in the host body varied from three to seven. The infected fish did not exhibit any recognizable pathological changes. Other species of fish caught at the same time, were free from the infection.



**Vegetative form:** The cysts are mostly spherical in form, and are covered by a tough resistant envelope composed of the connective tissue of the host. They are uniformly white in color, and have the variable dimensions of from 0.5 to 1.5mm. in diameter. In section, the protoplasm shows a coarsely reticulated structure without distinct differentiation. In all cysts of various sizes fully mature spores were only observed. The spore formation could not be worked out. Polysporous.

**Spore:** Broadly oval with a slightly truncated anterior end in front view (Fig. 628), lenticular in side or end view (Fig. 629). No intercapsular appendix is seen. The shell is rather thick, and shows about eight folds on the sutural edge, two of which located laterally being more conspicuous than others. The sutural ridge is rather fine. Two convergent polar capsules equal in size occupy the anterior half of the spore. The coiled polar filament becomes more distinctly visible with the addition of Lugol's solution, altho it is faintly observable in fresh state. Fresh spores extruded their polar filaments under the action of potassium hydrate solution. In some spores, the extruded filaments cross each other near the foramina. The preserved spores showed no extrusion of the filament as in the last species. The sporoplasm is extremely finely granulated. The iodophilous vacuole is comparatively large. When stained, the spore shows two nuclei in the sporoplasm. Dimensions of fresh material: length 10 to 11.5 $\mu$ , breadth 8.5 to 9.5 $\mu$ , thickness 6.5 $\mu$ , polar capsule 4.75 $\mu$  by 1.5 to 2 $\mu$ , length of polar filament 32 to 40 $\mu$ . Average dimensions of unstained preserved spores: length 9.5 $\mu$ , breadth 8 $\mu$ , polar capsule 4.75  $\mu$  by 2 $\mu$ .

**Remarks:** The habitat and the structure of the spores, lead the writer to record the species as a new species.

#### Genus HENNEGUYA Thélohan

1892	<i>Henneguya</i>	Thélohan	1892 : 167, 176
1895	<i>Henneguya</i>	Thélohan	1895 : 352

The characters of the genus are described on page 59.

Type species: *Henneguya psorospermica* Thélohan.

#### HENNEGUYA PSOROSPERMICA Thélohan

[Figs. 486, 487 and 496]

1895	<i>Henneguya psorospermica</i>	Thélohan	1895 : 353
1896	<i>Myxobolus psorospermica</i> s. str.	Cohn	1896 : 261
1899	<i>Henneguya psorospermica</i> <i>typica</i>	Labbé	1899 : 101
1905	<i>Henneguya psorospermica</i>	Nufer	1905 : 77, 185
1910	<i>Henneguya psorospermica</i>	Wegener	1910 : 81-82
1911	<i>Henneguya psorospermica</i> <i>typica</i>	Auerbach	1911 : 5, etc.

**Habitat:** Branchiae of *Esox lucius* L. and *Perca fluviatilis*; France,

Frisches and Kurisches Haff, Pregel, Masurische Seen (all the year round, but rarer in Winter) Switzerland.

Vegetative form: Thélohan's observations on the structure of the cyst, are as follows: The surface of the cyst is covered by a layer, homogeneous, refringent and deeply stained, with which the cyst comes in direct contact with the surrounding epithelial cells of the host. Inside of this layer, there is a "pseudoectoplasmic" zone, in which the protoplasm is dense at places, forming radiate irregular striations, enclosing numerous irregular masses which are composed of apparently the same substance that forms the external layer. Toward the central portion of the cyst, there are masses of spores (Fig. 496).

Cohn's descriptions are as follows: The purely white cyst is elliptical; length 1.15mm. and breadth 0.85mm. The seat is under the epidermis. It is surrounded by the host tissue with small, elongated and scattered nuclei. The outer layer of the cyst is a thin membranous protoplasm.

Wegener writes as follows: The white cysts are round or elliptical, usually on the upper end of the branchial lamella. Size of larger cysts, 1.5 to 2mm. long and 1.1 to 1.5mm. wide.

Spore: Elongated; anterior part fusiform and anterior end blunt. Polar capsules elongated and parallel to each other. Coiled polar filament visible in fresh conditions. Shell unstriated. Dimensions: total length  $40\mu$  in average, largest breadth  $7\mu$ , length of polar capsule 7 to  $8\mu$ .

Cohn's form is described by him as follows: Spore narrow with blunt anterior end. Sporoplasm with 6 horns (no figure to explain this expression!). When kept in water, sporoplasm takes round form and becomes highly refractive. Dimensions: length 29 to  $38\mu$ , length between the tip and the posterior margin of the cavity (15 to  $20\mu$ )  $18\mu$ , breadth 9 to  $10\mu$ , polar capsule (8 to  $11\mu$ )  $9\mu$  by  $2\mu$ , length of "starren Fäden"  $14\mu$ , length of tail 14 to  $18\mu$ .

Wegener's form is as follows: total length 35 to  $38\mu$ , breadth 7 to  $8\mu$ , length of the spore cavity  $15\mu$ , length of tail 15 to  $20\mu$ , polar capsule  $8\mu$  by 2 to  $3\mu$ .

#### HENNEGUYA TEXTA (Cohn) Labbé

1895	<i>Myxobolus textus</i>	Cohn	1895 : 38-39
1899	<i>Henneguya psorospermica texta</i>	Labbé	1899 : 101
1910	<i>Henneguya texta</i>	Wegener	1910 : 82-83

Habitat: Branchiae of *Perca fluviatilis* L.; Pregel, Frisches and Kurisches Haff (all the year round).

Vegetative form: Cohn observed as follows: Cyst distinctly elliptical. Length  $0.75\text{mm.}$ , breadth  $0.375\text{mm.}$  The cysts surrounded by a thick layer of the host tissue. In the peripheral portion of the cyst, the protoplasm exhibits a network-like structure which forms a fibrous structure further inside, crossing the cyst at right angles to the long axis of the cyst.

Wegener writes as follows: The white cysts are elongated, 1.2 to 1.8mm. long and 0.5 to 0.7mm. wide.

Spore: Cohn mentions dimensions exactly the same as those of *Henneguya psorospermica* and can not distinguish the two species by the spore.

Wegener gives the following dimensions: length 30 to 40 $\mu$ , breadth 7 to 8 $\mu$ , length of the cavity of spore 15 to 18 $\mu$ , length of tail 15 to 25 $\mu$ , polar capsule 8 $\mu$  by 2 to 3 $\mu$ .

#### HENNEGUYA MINUTA (Cohn) Labbé

[Figs. 488 and 489]

1895	<i>Myxobolus minutus</i>	Cohn	1895 : 39-40
1899	<i>Henneguya psorospermica</i> <i>minuta</i>	Labbé	1899 : 102

Habitat: Branchiae of *Perca fluviatilis* L.; Frisches Haff, Lesina.

Vegetative form: Cohn's description is as follows: Cysts oval and small, difficult to distinguish them from those of *Henneguya psorospermica*. Size, 130 $\mu$  by 115 $\mu$ . The parasite was met only once. But the number of the cysts was far greater than that of *Henneguya psorospermica*, often 5 to 6 on one lamella, reaching up to 200 cysts on a single gillarch.

Spore: Cohn gives the following dimensions: total length (28 to 45 $\mu$ ) about 36 $\mu$ , length from the tip to the end of cavity (20 to 28 $\mu$ ) about 26 $\mu$ , breadth 10 to 11 $\mu$ , thickness 8 $\mu$ , polar capsule 11 to 14 $\mu$  by 2 to 3 $\mu$ , length of polar filament 42 to 45 $\mu$ , length of tail (8 to 17 $\mu$ ) 12 $\mu$ . Cohn gives a figure (Fig. 489) of a spore with two vacuoles(?).

#### HENNEGUYA OVIPERDA (Cohn) Labbé

[Figs. 490 and 491]

1892		Weltner	1892 : 28-36
1895	<i>Myxobolus oviperdus</i>	Cohn	1895 : 40-41
1899	<i>Henneguya psorospermica</i> ovi- perda	Labbé	1899 : 102
1904	<i>Henneguya psorospermica</i> ovi- perda	Fuhrmann	1904 : 469-471
1911	<i>Henneguya psorospermica</i> ovi- perda	Auerbach	1911 : 5-22
1911	<i>Henneguya psorospermica</i> ovi- perda	Nemeczek	1911 : 146

Habitat: Ovary of *Esox lucius* L.; Switzerland, Berlin, Frisches Haff (all the year round), Upsala (May), Austria (December).

Vegetative form: Cohn writes as follows: No real cyst exists. The parasite occupies the ovum.

Auerbach, however, mentions the presence of cysts in the connective tissue and follicle epithelium of the ovary. Dimensions, 1mm. up to 5 or 6mm. in diameter.

Spore: Cohn states the form and dimensions are very much similar to those of *H. psorospermica*.

### HENNEGUYA LOBOSA (Cohn) Labbé

[Figs. 492 and 493]

1895	<i>Myxobolus lobosus</i>	Cohn	1895 : 42
1899	<i>Henneguya psorospermica lobosa</i>	Labbé	1899 : 102
1910	<i>Henneguya(?) lobosa</i>	Wegener	1910 : 83
1911	<i>Henneguya(?) lobosa</i>	Auerbach	1911 : 22-25

Habitat: Branchiae of *Esox lucius* L.; Frisches Haff, Pregel, Karlsruhe.

Vegetative form: Cysts irregular in shape, size up to 2.5mm.

Wegener noticed that the cyst resembles that of *Myxosoma dujardini* with the dimensions of 2.2 to 2.8mm. by 1 to 1.1mm.

Spore: Cohn gives the dimensions as follows: total length 30 to 40 $\mu$ , length from the tip to the posterior margin of cavity 11.5 to 15 $\mu$ , breadth 5 to 6.5 $\mu$ , polar capsules 6.5 to 8 $\mu$  by 2 to 2.5 $\mu$ , length of tail 22 to 28 $\mu$ .

Wegener's form: oval; length 35 to 40 $\mu$ , breadth 5 $\mu$ , polar capsule 6 to 7 $\mu$  by 2.5 to 3 $\mu$ , length of the cavity of spore 13 to 15 $\mu$ , length of tail 20 to 25 $\mu$ , the iodophilous vacuole could not be detected.

Auerbach gave the following dimensions: total length 30 $\mu$ , breadth 4 to 6 $\mu$ , length of polar capsule 6 $\mu$ , length of polar filament 48 to 54 $\mu$ .

Remarks: Wegener and Auerbach did not observe the iodophilous vacuole.

### HENNEGUYA PERI-INTESTINALIS Cépède

1906	<i>Henneguya psorospermica peri-intestinalis</i>	Cépède	1906 : 67
1907	<i>Henneguya psorospermica peri-intestinalis</i>	Cépède	1907 : 137
1912	<i>Henneguya psorospermica peri-intestinalis</i>	Parisi	1912 : 295

Habitat: Intestine of *Esox lucius* L.; Lac du Bourget, Pavia. (June).

Vegetative form: Cysts.

Spore: Cépède mentions that it resembles that of *Henneguya psorospermica*.

### HENNEGUYA MEDIA Thélohan

[Figs. 494 and 495]

1890		Thélohan	1890 : 198-200
1892	<i>Henneguya media</i>	Thélohan	1892 : 177
1894	<i>Myxobolus medius</i>	Gurley	1894 : 248
1895	<i>Henneguya media</i>	Thélohan	1895 : 353
1898	<i>Henneguya media</i>	Doflein	1898 : 342

Habitat: Renal tubules of kidney and ovary of *Gasterosteus aculeatus* and *G. pungitius* L.; France. Mixed infection with *Sphaerospora elegans*.

Vegetative form: Rounded or elongated. In larger individuals, clear differentiation of protoplasm. Monosporous (?) and polysporous.

Spore: Fusiform. Shell striated. A vacuole in sporoplasm. Dimensions: length 20 to 24 $\mu$ , breadth 5 to 6 $\mu$ , polar capsules 4 to 5 $\mu$ . Tail short.

#### HENNEGUYA BREVIS Th  lohan

1854		Lieberk��hn	1854 : 357
1892	<i>Henneguya brevis</i>	Th��lohan	1892 : 177
1895	<i>Henneguya brevis</i>	Th��lohan	1895 : 354

Habitat: Similar to *H. media* Th  lohan.

Vegetative form: Undescribed.

Spore: Fusiform with short tail. Dimensions: length 14 to 15 $\mu$ , breadth 5 to 6 $\mu$ , polar capsules 1.4 to 5 $\mu$ , tail 4 to 5 $\mu$  long.

#### HENNEGUYA SCHIZURA (Gurley) Labb  

[Figs. 497 to 499]

1841		M��ller	1841 : 477-478
1893	<i>Myxobolus schizurus</i>	Gurley	1893 : 417
1894	<i>Myxobolus schizurus</i>	Gurley	1894 : 255
1899	<i>Henneguya schizura</i>	Labb��	1899 : 102-103

Habitat: In cellular tissue of the eye muscles, in that of the sclerotic, and in that between the sclerotic and choroid of *Esox lucius* L.; Germany, U. S. A.

Vegetative form: Cysts white; membrane delicate; 0.44 to 1.09mm. in diameter.

Spore: Oval. Dimensions: length 12 $\mu$ , breadth 6 $\mu$ , thickness one-half the breadth, tail 3 to 4 times length of the body.

#### HENNEGUYA CREPLINI (Gurley) Labb  

[Figs. 500 to 503]

1842		Creplin	1842 : 61-63
1894	<i>Myxobolus creplini</i>	Gurley	1894 : 248-249
1899	<i>Henneguya creplini</i>	Labb��	1899 : 103
1910	<i>Henneguya creplini</i>	Wegener	1910 : 84

Habitat: Branchiae of *Acerina cernua* L.; Pregel (March), Frisches and Kurisches Haff.

Vegetative form: Wegener describes as follows: Cysts, usually elongated oval and are located at the end of branchial lamella. Color white. Size 1 to 1.1mm. by 0.5mm. During winter, the cyst has only pansporoblasts, but no fully grown spores.

Spore: Creplin writes as follows: Elongated elliptical. Length 1/120"', breadth 1/360"', tail about as long as or a little longer than the body.

Wegener's form: elongated spindle shape; length 20 $\mu$ , breadth 8 to 9 $\mu$ , polar capsule 8 $\mu$  by 2 to 3 $\mu$  (parallel to each other).

Remarks: Wegener thinks that the present species and *Henneguya acerinae* Schröder, are one and the same species, and that the differences between the dimensions are due to the miscalculation of measurement in lines given by Creplin on the part of Gurley and Labbé.

### HENNEGUYA LINEARIS (Gurley) Labbé

[Fig. 504]

1841		Müller	1841 : 489
1893	<i>Myxobolus linearis</i> (part)	Gurley	1893 : 417
1894	<i>Myxobolus linearis</i>	Gurley	1894 : 255
1899	<i>Henneguya linearis</i>	Labbé	1899 : 103

Habitat: Membrane lining branchial cavity of *Pimelodus sebae* Cuv. et Val., branchiae of *Platyostoma fasciatum* L.; South American rivers.

Vegetative form: Not described.

Spore: Very narrow. Length 3 to 4 times breadth.

### HENNEGUYA GURLEYI Kudo

[Fig. 505]

1893	<i>Myxobolus linearis</i> (part)	Gurley	1893 : 417
1894	<i>Myxobolus</i> cf. <i>linearis</i>	Gurley	1894 : 253-254
1899	<i>Henneguya linearis</i> var.	Labbé	1899 : 103

Habitat: Base of spines of the second dorsal fin of *Ameiurus melas* Raf.; Iowa (Storm Lake) (August).

Vegetative form: Spherical cysts, 1mm. in diameter.

Spore: Lanceolate. Dimensions: length of the body  $19\mu$ , width 5 to  $6\mu$ , thickness about  $3\mu$ .

Remarks: The species is most probably different from *Henneguya linearis* judging from the difference in the form and structure of spores, the seat of infection, and host species. Hence, it is recorded here as an independent species.

### HENNEGUYA STRONGYLURA (Gurley) Labbé

[Fig. 506]

1841		Müller	1841 : 480
1894	<i>Myxobolus strongylurus</i>	Gurley	1894 : 249
1899	<i>Henneguya strongylura</i>	Labbé	1899 : 103

Habitat: Skin of cephalic region of *Synodontis schall* Bl. Schn.; Nile.

Vegetative form: Cysts over 2.18mm. in diameter.

Spore: Dimensions: length of the body  $9\mu$ , breadth  $5.4\mu$ . Tail always undivided. Two polar capsules of equal size.

## HENNEGUYA MONURA (Gurley) Labbé

[Fig. 507]

1880		Ryder	1880 : 211-212
1893	<i>Myxobolus monurus</i>	Gurley	1893 : 416
1894	<i>Myxobolus monurus</i>	Gurley	1894 : 249-250
1899	<i>Henneguya monura</i>	Labbé	1899 : 103

Habitat: Subcutaneous intermuscular tissue of *Aphredoderus sayanus* Gill.; New Jersey (Woodbury).

Vegetative form: Cysts, lenticular, large, white, opaque and numerous (20). Membrane thin.

Spore: Lenticular or slightly obovate. Tail 2 to 3 times longer than the body.

## HENNEGUYA KOLESNIKОВI (Gurley) Labbé

[Fig. 508]

1886		Kolesnikov	1886 : 242-248
1894	<i>Myxobolus kolesnikov</i>	Gurley	1894 : 256-257
1898	<i>Myxobolus bicaudatus</i> (part)	Zschokke	1898 : 602-604, 646-655, 699-703
1899	<i>Henneguya kolesnikov</i>	Labbé	1899 : 103-104

Habitat: Interstitial connective tissue of the thoracic and intercostal muscles of *Coregonus lavaretus* L.; Russia.

Vegetative form: Cysts numerous (80), spherical or oval; length 10 to 30mm., breadth 7 to 20mm.

Spore: Oval with a pointed anterior end. Tail three times longer than the body.

Remarks: Zschokke thinks the present species is identical with *Henneguya zschokkei*. But the evidence is not clear enough to bring one to agree with him due to the incomplete description of the present species.

## HENNEGUYA MACRURA (Gurley) Thélohan

[Figs. 509 to 512]

1893		Evermann	1893 : 76
1894	<i>Myxobolus macrurus</i>	Gurley	1894 : 250-253
1895	<i>Henneguya macrura</i>	Thélohan	1895 : 354

Habitat: Subcutaneous connective tissue of head of *Hybognathus nuchalis* Ag.; Neches River, Texas (November, temperature of water 9°.4C.) Of frequent occurrence.

Vegetative form: Cysts, elongated 6mm. by 2mm. or less.

Spore: Rounded oblong. Dimensions: length 10 to 11 $\mu$ , breadth 6 to 8 $\mu$ , thickness 4 $\mu$ . Shell-valves unequally convex. Tail 30 to 40 $\mu$ .

## HENNEGUYA ZSCHOKKEI (Gurley) Doflein

[Fig. 513]

1884		Zschokke	1884 : 234-235
1894	<i>Myxobolus</i> (?) <i>zschokkei</i>	Gurley	1894 : 244
1898	<i>Myxobolus bicaudatus</i> (part)	Zschokke	1898 : 602-607, 646-655, 699-703
1898	<i>Myxobolus bicaudatus</i>	Zschokke	1898a : 213-214
1901	<i>Henneguya zschokkei</i>	Doflein	1901 : 202
1904	<i>Henneguya zschokkei</i>	Hofer	1904 : 56
1905	<i>Henneguya zschokkei</i>	Nufer	1905 : 77, 185

Habitat: Subcutaneous and superficial intermuscular tissue of *Coregonus fera*, *C. schinzii* Fatio, *C. hiemalis* Jur. and muscular tissue and branchia of *C. wartmanni nobilis* and *C. exiguus albellus*; Neuchâtel See, Zurich See, Genfer-see, Thuner-see, Vierwaldstätter-see.

Vegetative form: Zschokke writes as follows: Cysts rounded or oval surrounded by a compact membrane with many nuclei. The largest 32mm. by 16mm. Protoplasm granular. Polysporous.

Spore: Rounded oval in front view; broad elliptical in side view. Anterior end rounded; posterior end tapering, forming tail. Sutural ridge distinct. Tail is either bifurcated along the entire length or a single form, no intermediate form being observed. Dimensions: total length 55 $\mu$ , length of the body 10 $\mu$ , breadth 7 $\mu$ , length of tail 4 to 5 times the length of the spore-body, length of polar filament 6 to 10 times that of the body of the spore.

Remarks: Zschokke thinks that *Henneguya kolesnikovii*, *H. zschokkei* and *H. sp.* Gurley are one and the same species, for which he proposed the name *Myxobolus bicaudatus*.

## HENNEGUYA sp. (Gurley) Labbé

[Fig. 514]

1886		Benecke	1886 : 211
1894	<i>Myxobolus sp. inc.</i>	Gurley	1894 : 244
1899	<i>Henneguya sp.</i>	Labbé	1899 : 104
1904	<i>Henneguya sp.</i>	Hofer	1904 : 51

Habitat: Integument (?) of *Leuciscus rutilus* L. The parasites formed boil-like enlargement in the skin.

Vegetative form: Not described.

Spore: Not described.

## HENNEGUYA sp. (Gurley) Labbé

1874		Claparède	1874 : 114
1894	<i>Myxobolus sp. inc.</i>	Gurley	1894 : 253
1898	<i>Myxobolus bicaudatus</i> (part)	Zschokke	1898 : 602-607, 646-655, 699-703
1899	<i>Henneguya sp.</i>	Labbé	1899 : 104

Habitat: Branchial-arches of *Coregonus fera*; Genfer-see.



Vegetative form: One cyst, 1mm. in diameter.

Spore: Tail short. Zschokke quotes: length 8 to 10 $\mu$ .

Remarks: According to Zschokke, this species is identical with *H. zschokkei*.

### HENNEGUYA TENUIS Vaney et Conte

[Fig. 515]

1901 *Henneguya tenuis* Vaney and Conte 1901 : 103-106

Habitat: Connective tissue of alimentary tract of *Acerina cernua* L.; Lyon (February).

Vegetative form: Numerous cysts particularly in the pyloric coecum. Usually spherical. Size: 30 to 150 $\mu$  in diameter.

Spore: Oval and small. Tail short. Two polar capsules at the anterior end. Sporoplasm with a nucleus, rod-shaped, with somewhat enlarged ends which is located at right angles to the longitudinal axis. Iodinophilous vacuole could not be traced. Dimensions: length 4 $\mu$ , breadth 2 $\mu$ .

### HENNEGUYA NÜSSLINI Schuberg et Schröder

[Figs. 516 and 517]

1905 *Henneguya nüsslini* Schuberg and Schröder 1905 : 56-59

Habitat: Subcutaneous connective tissue at the base of dorsal fin of *Trutta fario* L.; Gutach.

Vegetative form: Trophozoites form cysts (2 cysts found). Cysts lenticular, 1.5 to 2mm., surrounded by many concentric layers of fibrous connective tissue. Cysts containing only mature spores.

Spore: Broad oval form, flattened. Anterior end rounded. Tail at the posterior end. Shell somewhat thick, often shows sutural ridge. Tail filaments two. A "dark part" which in side-view is of triangular form, runs into the tail. Sporoplasm, occupying the posterior half of the spore, projects a narrow portion between the polar capsules beyond the middle of the capsules. Sporoplasm, uniformly granular, contains an iodophilous vacuole and one, sometimes two nuclei connected by nuclear bridge. Polar capsules, pyriform, opening independently. Coiled polar filament observable, coiled 6 to 7 times. Dimensions: length excluding tail 12 $\mu$ , length with tail 32 $\mu$ , breadth 8 to 9 $\mu$ , polar capsules 5 $\mu$  by 3 $\mu$ , length of polar filament 4 to 5 times longer than that of spore excluding tail (48 to 60 $\mu$ ).

### HENNEGUYA LÉGERI Cépède

[Figs. 518 to 523]

1905	<i>Henneguya légeri</i>	Cépède	1905 : 905-913
1906	<i>Henneguya légeri</i>	Cépède	1906 : 66
1913	<i>Henneguya légeri</i>	Cépède	1913 : 302-305

Habitat: Urinary bladder of *Cobitis barbatula* L.; Isère (January).

**Vegetative form:** Young trophozoites subcircular, irregularly elliptical or elongated with distinct differentiation of protoplasm into ectoplasm and endoplasm. Plasmotomic multiplication takes place during winter months, when no spore is formed.

**Spore:** Oval with short tail, mostly bifurcated at the free end. The anterior end is more rounded, occasionally acuminate. Two polar capsules of equal size. Coiled polar filament distinct in vivo. Sporoplasm granular, contains two nuclei and a vacuole. The spore often shrinks in fresh conditions, probably owing to the poorly developed thin valves. Dimensions of spores mounted in balsam: length variable. Examples: Total length  $22.5\mu$ , tail  $8.5\mu$ ; total length  $19.5\mu$ , tail  $8\mu$ ; length of main part  $8.5\mu$ , breadth (comparatively constant)  $6\mu$ .

#### HENNEGUYA ACERINAE Schröder

[Figs. 525 and 526]

1906	<i>Henneguya acerinae</i>	Schröder	1906 : 186-196
1910	<i>Henneguya creplini</i>	Wegener	1910 : 84
1911	<i>Henneguya acerinae</i>	Nemeczek	1911 : 155

**Habitat:** Branchiae of *Acerina cernua* L., *Aspro zingel* Cuv., *Lucioperca lucioperca* L. and *L. sandra* Cuv. (?); Heidelberg (Necker), Apatin, Komitat Baco-Bodrog, Hungary (May).

**Vegetative form:** Schröder describes as follows: Rounded or spherical cysts in the connective tissue of branchial lamella. Full-grown cysts up to  $300\mu$  in diameter. Protoplasm is differentiated into ectoplasm and endoplasm. Ectoplasm shows fine radial striations. Endoplasm granular, contains many nuclei, especially lying in the middle portion. Well developed cyst, containing only spores, is surrounded by a membrane. On the surface of the ectoplasm, numerous edge-like elevations, branched and joining together, were recognized. Polysporous.

Nemeczek observed the largest cyst, spherical and  $600\mu$  in diameter.

**Spore:** Pyriform in front view; flattened. The anterior end is more or less blunt. Shell uniformly thin. Sutural edge slightly enlarged. Sporoplasm finely granular, contains an iodophilous vacuole and two nuclei. Polar capsules approximated closely, each having an independent opening. Dimensions: length 20 to  $22\mu$ , breadth 8 to  $9\mu$ , thickness 6 to  $7\mu$ , length of tail 50 to  $60\mu$ , polar capsules  $10\mu$  by 2 to  $3\mu$ , length of polar filament 80 to  $90\mu$  (water and nitric acid).

Nemeczek's form is as follows:

The tail is bifurcated along its entire length. In one case (May, 1909), however, all the spores had no bifurcated tail, while the polar capsules were of unequal size. Dimensions in fresh state: total length 37.6 to  $41.8\mu$ , length, excluding tail 12.6 to  $16.8\mu$ , breadth  $4.5\mu$ , length of polar capsule 6.3 to  $8.4\mu$ , length of polar filament  $67\mu$ , length of tail  $25\mu$ .

Nemeczek observed two more different (?) forms. One form found in *Lucioperca sandra*, tho the size differs from the dimensions given by Schröder, is thought to be identical with the present species. Another form in the branchiae of *Aspro zingel*, which is also to be one and the same species with the present species has the following dimensions: total length  $35\mu$ , length of spore excluding tail  $15\mu$ , breadth  $5\mu$ , length of polar capsule  $6\mu$ , length of tail  $20\mu$ .

### HENNEGUYA GIGANTEA Nemeczek

[Figs. 527 to 535]

1911	<i>Henneguya gigantea</i>	Nemeczek	1911 : 146-154
1914	<i>Henneguya gigantea</i>	Georgévitch	1914 : 387-409

Habitat: Branchiae of *Lucioperca sandra* Cuv.; Apatin, Komitat Bacs-Bodrog, Hungary, Petrograd. Nemeczek mentions that the infection takes place only among young fish.

Vegetative form: Cysts numerous and of conspicuous size in the free end of branchial lamella. In average, each gill-arch has about 100 cysts which are of creamy color. Young cysts 400 to  $450\mu$  in diameter. They gradually begin to increase the size, from autumn until toward the end of spring, during which period, the contents remaining in the stages of pansporoblasts formation. Older cysts rounded spindle shape with the length of 4 to 7mm. and the breadth of 2 to 3mm. The connective tissue and epithelial cell layers form the cyst membrane. The connective tissue either simply surrounds the parasite or branches in the surface of the parasite, increasing in thickness and forming more or less enclosed chambers of the parasite. The membrane of the cyst which contains mature spores is usually very thin. Throughout the growth of the cyst, "chromatoid body" is seen in the endoplasm, which appears first as a filiform structure, stained deeply with nuclear stain. Later they gather together and form a compact body, situated excentrically. Fine branches, from it become directed toward the surface of the body, anastomosing each other so that a network is formed on the surface of the cyst. The latter develops small ovoidal or columnal bodies ( $1.2\mu$  long and about  $1\mu$  wide), which are arranged radially and densely. The number and quantity of these bodies increase in proportion to the number of propagative nuclei and they begin to disappear, first in the central portion, then in the periphery, so that in fully grown cysts (in summer months) these chromatoidal bodies are more rudimentary. Differentiated protoplasm is only recognized in young individuals, in which case ectoplasm is homogeneous and endoplasm reticular. Polysporous.

Spore: Nemeczek gives the following accounts.

Spindle shape, with truncate anterior end and very long thread like tail at the posterior end. The tail seems split into two at about the middle part of its length. Gentian violet stains the tail so intensively that its entire length could easily be made out. Dimensions: total length 87.5 to 110.5 $\mu$ , length of the body 10.5 $\mu$ , breadth 5 $\mu$ , length of tail 77 to 100 $\mu$ , length of polar capsule 5 $\mu$ , length of polar filament 70 $\mu$  (pressure or dessication followed by immersion in water).

Georgévitch's form: length excluding tail 15 $\mu$ , breadth 6 $\mu$ , length of tail 75 $\mu$ , length of polar capsule 6 $\mu$ , length of polar filament 75 $\mu$ , diameter of the iodophilous vacuole 4 $\mu$ .

Remarks: Nemeček mentions that from October on, cysts had no spores, only containing propagative cells. The velocity of the development of spores depends upon the temperature of water.

Georgévitch worked out the spore formation of the species and observed that the binucleated sporeplasm emerged from the posterior end of the spore.

#### HENNEGUYA (?) sp. Nemeček

[Figs. 536 to 539]

1911 *Henneguya* sp.

Nemeček

1911 : 157-159

Habitat: Branchiae of *Abramis brama*; Komorn, Komitat Komorn, Hungary (March).

Vegetative form: Cysts in the branchiae.

Spore: Besides normal spores of *Myxobolus rotundus* (page 149), spores of *Henneguya* type in small number were found. The anterior part of these spores resembles that of the species mentioned above, while the breadth is much smaller (8 $\mu$ ) than the latter. Majority of spores have a thread like tail, 10 to 15 $\mu$  long, which was often bifurcated. An iodophilous vacuole was fairly marked.

Remarks: It is placed here as a species of *Henneguya* by reason of the bifurcate tail.

#### HENNEGUYA GASTEROSTEI Parisi

[Figs. 540 to 543]

1912 *Henneguya gasterostei*

Parisi

1912 : 296-297

Habitat: Kidney of *Gasterosteus aculeatus* L.; Lago di Garda (February).

Vegetative form: Rounded or oval, usually with two, but rarely with four spores. Ectoplasm thin and hyaline. Endoplasm contains numerous granules, most probably of fatty nature and decreasing in number as spores grow. Free full-grown spores were seen abundantly in the connective tissue of renal tubules, glomeruli, etc. Disporous and polysporous.

Spore: Oval with slightly attenuated anterior end; posterior end tapering into tails, which end in one point or bifurcated; asymmetrical in shape, one valve is more curved than the other. This asymmetry of the shell-valves in profile enables the present species to be distinguished from other species. Shell striated longitudinally. Two polar capsules pyriform and well developed, reaching to the middle of the spore. Sporoplasm with a round iodophilous vacuole. Dimensions: total length 38 to 48 $\mu$ , length of the cavity of the spore 15 $\mu$ , breadth 6 to 7.5 $\mu$ , polar capsules 7.5 to 9 $\mu$  by 3 to 3.5 $\mu$ , length of polar filament 50 $\mu$ .

#### HENNEGUYA NEAPOLITANA Parisi

[Figs. 544 and 545]

1912    *Henneguya neapolitana*    Parisi    1912 : 297-298

Habitat: Connective tissue of the renal tubule of kidney of *Box salpa* C. et V.; Napoli (August).

Vegetative form: Small cyst (40 to 50 $\mu$  in diameter) surrounded by thin membrane, containing a number of spores, numerous pigment granules and coarse yellowish globules.

Spore: Oval, slightly flattened. Anterior end rounded when seen from the front, but attenuated in profile. Shell tapering into a long fine tail posteriorly. The fine distal portion of the tail wraps around the thicker part. Two polar capsules, pyriform, occupying the anterior half of the cavity of the spore, cross each other when seen from the front. Sporoplasm finely granular with two nuclei, the iodophilous vacuole being hardly visible. Dimensions: total length 50 to 60 $\mu$ , length of the cavity of spore 8.5 to 9.5 $\mu$ , breadth 8.5 to 9.5 $\mu$ , internal breadth 6.3 to 7 $\mu$ , thickness 8 $\mu$ , polar capsules 4.7 to 5.5 $\mu$  by 3 $\mu$ .

#### HENNEGUYA WISCONSINENSIS Mavor et Strasser

[Figs. 558 and 559]

1916    *Henneguya wisconsinensis*    Mavor et Strasser    1916 : 676-682

Habitat: Urinary bladder of *Perca flavescens*; Lake Mendota, Wisconsin (April).

Vegetative form: Trophozoites are usually elongated and have the general form and shape of a limax ameba. It may reach a size of 300 $\mu$  by 70 $\mu$ . Clear differentiation of ectoplasm and endoplasm. Pseudopodia lobose. Two spores are formed in each pansporoblast. Polysporous.

Spore: Ovoid, bilaterally symmetrical, and have a bifurcated caudal process. Two polar capsules at anterior end. Coiled polar filament visible *in vivo* (5 windings). Dimensions: length excluding tail 11.5 $\mu$ , breadth 7 $\mu$ , tail 9.6 $\mu$ , polar capsules 3.5 $\mu$  by 2.5 $\mu$ , length of filament 33 $\mu$ .

## HENNEGUYA BRACHYURA Ward

[Figs. 650 to 653]

1919 *Henneguya brachyura* Ward 1919 : 57

**Habitat:** In the cartilaginous fin ray of the caudal fin of *Notropis anogenus*; Put-in-Bay, Lake Erie (August). The species was found encysted in the same fish which was heavily infected by *Myxobolus aureatus*.

**Vegetative form:** Cysts rounded with slightly irregular contour imbedded in the fin ray. The size varies from  $160\mu$  in diameter up to  $360\mu$  by  $240\mu$ . No particular cyst membrane could be recognized. The differentiation of the protoplasm into ectoplasm and endoplasm is distinct. The ectoplasm covering the entire surface of the parasite as a layer 4 to  $6\mu$  thick, shows structure of a very finely granular nature. The endoplasm coarsely alveolar, is filled with mature spores in the central portion, while numerous nuclei and young spores in various developmental stages are present at the peripheral portion. Polysporous.

**Spore:** Rounded oval in front view; spindle shape with symmetrically built valves in profile. Shell rather thick. Sutural ridge fairly well marked; sutural edge exhibiting a variable number of folds (8 to 10). Two pyriform polar capsules are usually of the same size and form. The tail is a single process, usually more or less bent or irregularly curved, very rarely being straight. In general, it is sinuous with two or three shallow curves and is rather short, tapering gradually to a point. In young spores which are less deeply stained by any stain, various developmental stages of the tail are readily recognized. Giemsa solution stains the shell proper in clear blue, while the tail takes on a beautiful pink color, a distinct difference in affinity for dyes between the material in the tail and the shell. It seems probable that the tail of this type is entirely different in its development from that of the ordinary bifurcated type. Dimensions in section: length 10 to  $11.5\mu$ , breadth 8 to  $8.75\mu$ , thickness 4 to  $5\mu$ , polar capsules 3 to  $4\mu$  by  $2\mu$ , length of the tail up to  $17\mu$ .

## HENNEGUYA SALMINICOLA Ward

[Figs. 654 to 656]

1914	? <i>Henneguya zschokkei</i>	Zschokke and Heitz	1914 : 200-201
1919	<i>Henneguya salminicola</i>	Ward	1919 : 59

**Habitat:** In the sub-dermal tissue of *Onchorhynchus keta* and *O. kisutch* (Zschokke and Heitz, Kamtschatka) and in the connective tissue in body muscles of *Oncorhynchus keta*, Stickeen River, Alaska (Ward, September). The last named author undertook a careful examination of a part of the infected tissue preserved in formol. The species forms conspicuous cysts in the muscle from the sub-peritoneal to the sub-dermal connective tissue, tho all are sub-peritoneal in position.

**Vegetative form:** Ward describes as follows: The whitish opaque cysts are pyriform, and fairly uniform in size (3 to 6mm. in diameter). The cyst is covered by numerous layers of connective tissue which form a tough membrane around the parasite. The cyst contains young spores in various stages of development, which showed that two spores are formed in one pansporoblast, and mature spores thickly massed together in the central area. Polysporous.

**Spore:** Oval with rounded anterior and more or less attenuated posterior ends; elliptical in profile with attenuated anterior end. Shell smooth. Sutural edge exhibits folds variable in number (usually 6 to 7). Tail double, composed of two fine and equal halves which are the prolongation of the shell valves. The processes usually run roughly parallel to each other. Two pyriform polar capsules are of slightly different dimensions. Coiled polar filament is indistinct in preserved unstained specimens. Sporoplasm finely granular, shows a large iodophilous vacuole. Dimensions of stained and mounted spores: total length  $47\mu$  ( $42.75$  to  $52.44\mu$ ), length of the main part  $12\mu$  ( $11.97$  to  $14.25\mu$ ), breadth  $8\mu$  ( $7.12$  to  $8.43\mu$ ), thickness  $4.78\mu$ , length of tail  $35\mu$  ( $30.78$  to  $38.19\mu$ ), polar capsule  $3.70$  to  $4.55\mu$  by  $1.59$  to  $2.85\mu$ .

**Remarks:** Zschokke and Heitz (1914) observed a species from Kamtschatka, which they thought to be identical with *Henneguya zschokkei* (page 165). The writer is inclined to think that the species is identical with the species just described from Alaska.

#### HENNEGUYA MIYAIRII nov. spec.

[Fig. 524]

1909 *Henneguya* sp.

Miyairi

1909 : 127-129

**Habitat:** Subcutaneous tissue of head of *Carassius auratus* L.; Fukuoka (Nippon).

**Vegetative form:** Trophozoites form cysts and are also found in the condition of diffuse infiltration around the cysts. Cyst-membrane fibrous and thin. Ectoplasm and endoplasm fairly well differentiated, though the border line is not sharply marked. At the periphery of endoplasm, pansporoblasts with 7 to 12 nuclei are present (Two spores are formed in each pansporoblast?). Polysporous.

**Spore:** Oval, with broadly rounded anterior and slightly elongated posterior ends, the latter ending in long and fine tails. Two polar capsules at the anterior portion, are pyriform, small and convergent. Sporoplasm with an iodophilous vacuole. Dimensions: length  $12\mu$ , breadth  $8\mu$ , length of the tails 10 to  $30\mu$ , length of polar filaments 23 to  $40\mu$ .

**Remarks:** As the description gives the details by which the species can be distinguished from other species, the writer establishes it on an independent basis.

## HENNEGUYA MICTOSPORA nov. spec.

[Figs. 546 to 557]

Habitat: Urinary bladder of *Lepomis cyanellus* Raf., *L. humilis* Gir. and *Micropterus salmoides* Lac.; Stony Creek, Ill. (November).

In one out of three (6.5 to 8cm. long) of the first, in one out of two (7 and 9.5cm. long) of the second and in one of the third species, examined in the middle of November, was found the present form. None showed a heavy infection, a number of scattered trophozoites and spores being observed. The host did not show any pathological change.

Vegetative form: Polymorphous. Generally rounded or elongated oval. In small monosporous and disporous forms, the tail of the spores developed inside, is extruded from the body, so that these trophozoites show long processes (Figs. 546, 553, 555). Pseudopodia lobose, and extruded from the entire surface of the body (Fig. 547), tho sometimes they are well formed at one end of the body. Protoplasm is differentiated distinctly into ectoplasm and endoplasm. Ectoplasm is homogeneous and hyaline, forming the outer layer. Endoplasm is of reticular structure. The body is colorless, often yellowish, when the endoplasm is loaded with numerous yellowish coarse granules. The size varies from 6 or 7 $\mu$  up to 60 $\mu$ . In a rounded form of 38 $\mu$  in longest diameter, five pansporoblasts, each developing two spores and many nuclei were observed. In another oval form of 45 $\mu$  by 60 $\mu$  in size, numerous nuclei were stained, showing that no development of pansporoblast has yet taken place. Disporous, polysporous and monosporous, tho of rare occurrence.

Spore: Broad spindle shape with attenuated anterior end. Shell rather thin. Each valve has 6 to 8 longitudinal striations on the surface. A long tail composed of two halves, is developed at the posterior end. Two pyriform polar capsules with distinctly visible coiled polar filament opens at the anterior tip. Sporoplasm, finely granular, contains an iodophilous vacuole which is made distinctly visible by treating with Lugol's solution. When stained two typical nuclei are recognized in the sporoplasm. Dimensions of the fresh spores: length excluding tail 13.5 to 15 $\mu$ , breadth 8 to 9 $\mu$ , thickness 6 to 7.5 $\mu$ , length of tail 30 to 35 $\mu$ , often up to 40 $\mu$ , polar capsule 5 to 6 $\mu$  by 3 $\mu$ , length of polar filament 40 $\mu$ .

## Genus HOFERELLUS Berg

1898	<i>Hoferellus</i>	Berg	1898 : 41
1898	<i>Hoferia</i>	Doflein	1898 : 288-289

The characters of the genus are described on page 59.

Type and only species: *Hoferellus cyprini* Doflein.



## HOFERELLUS CYPRINI Doflein

[Figs. 577 to 581]

1898	<i>Hoferia cyprini</i>	Doflein	1898 : 289-290
1908	<i>Hoferellus cyprini</i>	Mercier	1908 : LIII-LIV
1910	<i>Hoferellus cyprini</i>	Plehn	1910 : 20-22

Habitat: In lumen and epithelial cells of renal tubules of kidney of *Cyprinus carpio* L.; France and Germany.

Vegetative form: Young trophozoites live in epithelium. Adults free in the urinary tubules. Form rounded or oval. No clear differentiation of protoplasm. Pseudopodium unobserved. Endoplasm contains numerous granules and many nuclei. Each pansporoblast forms two spores. Smaller individuals 20 to 30 $\mu$  in diameter. Polysporous.

Spore: Pyramidal with two short tail-like processes at the posterior end, which are formed from the shell-valves like those of *Henneguya*. Between these two processes, rarely small protoplasmic pointed processes occur. Each shell-valve has 9 to 10 longitudinal striations on it. Two polar capsules at the anterior part, show clearly the coiled polar filaments. Sporoplasm has two nuclei and an iodophilous vacuole. Dimensions: total length 10 to 12 $\mu$ , breadth 8 $\mu$ , tail-process 2 $\mu$  long, polar capsule 3 $\mu$  long.

## MYXOSPORIDIA GENERA ET SPECIES INCERTAE

Gen. et spec. incert. Leydig

1851		Leydig	1851 : 222
1894	Gen. et spec. incert.	Gurley	1894 : 186

Habitat: Cysts in the root of tongue of *Chondrostoma nasus* L.; Germany.

Gen. et spec. incert. Leydig

1851		Leydig	1851 : 222
1894	Gen. et spec. incert.	Gurley	1894 : 186

Habitat: Heart (auriculo-ventricular valve) of *Leuciscus rutilus* L.

Gen. et spec. incert. Leydig

1851		Leydig	1851 : 223
1894	Gen. et spec. incert.	Gurley	1894 : 186

Gen. et spec. incert. Heckel et Kner

1851		Heckel and Kner	1851 : 12
1894	Gen. et spec. incert.	Gurley	1894 : 186-187

Habitat: Branchiae of *Lucioperca lucioperca* L.; Austria.

Gen. et spec. incert. Borne

1886		Borne	1886 : 211
1894	Gen. et spec. incert.	Gurley	1894 : 187

Habitat: *Scomber scombrus* L.

## Genus incert. MERLUCII Perugia

[Figs. 582 and 583]

1891	<i>Myxosporidium merlucii</i>	Perugia	1891 : 22-24
1894	<i>Myxobolus</i> ? <i>merlucii</i>	Gurley	1894 : 242-243
1899	<i>Myxobolus merlucii</i>	Labbé	1899 : 100

Habitat: Gall-bladder of *Merlucius merlucius* L.; Italy.

Vegetative form: Various form. No differentiation of protoplasm. Disporous (?).

Spore: Oval, with two polar capsules.

Remarks: The species was placed in the genus *Myxobolus* by previous authors. The figures given by Perugia show that the spores are at least dimorphous. From the habitat and the disporous characters, one should place it rather in one of the genera of the Family Ceratomyxidae.

## Genus incert. CONGRI Perugia

[Figs. 584 and 585]

1891	<i>Myxosporidium congrei</i>	Perugia	1891 : 24-25
1894	Genus incert. <i>congrei</i>	Gurley	1894 : 182
1912	<i>Myxobolus congrei</i>	Parisi	1912 : 284

Habitat: Gall-bladder of *Conger conger* L.; Genova.

Vegetative form: Floating in the bladder. Form variable. Movements incessant, slow and ameboid.

Spore: Not described.

## Gen. et spec. incert. Linton

[Fig. 590]

1891		Linton	1891 : 359-361
1894	Gen. et spec. incert.	Gurley	1894 : 182-183

Habitat: Subcutaneous tissue of *Notropis megalops* Raf.; Ohio (Black River; September, October).

Vegetative form: Cysts. Globular, discrete or aggregated into clusters, white, with minute patches of black pigment from host; size varying from 2.5mm. (single cyst) to 7mm. by 5mm. (clusters); cyst-membrane composed of connective tissue.

Spore: Top-shaped, somewhat flattened; with pointed anterior and broadly rounded posterior end. Shell thick, with elevated sutural ridge. Polar capsules could not be detected. Protoplasm finely granular. Dimensions: length 17 $\mu$ , breadth 10 $\mu$ , thickness 6 $\mu$ .

Remarks: The cysts and figures of spores given by Linton suggest that it is most probably a unicapsular *Myxobolus*. As Linton could not detect (?) the polar capsule, tho his figures faintly show the said structure, it is placed in this group.

## Gen. et spec. incert. Mingazzini

1892	Mingazzini	1892 : 398
1899	Labbé	1899 : 113

Habitat: Ovarian egg of *Lacerta* sp.

Vegetative form: Ameboid with hyaline pseudopodia and granular protoplasm.

Spore: Not observed.

## Gen. et spec. incert. Nufer

1905	<i>Myxobolus</i> sp.	Nufer	1905 : 71, 77, 79, 85, 186
------	----------------------	-------	----------------------------

Habitat: In the connective tissue of branchia of *Chondrostoma nasus*; Lake of Lucerne. A single cyst in a single host fish.

Vegetative form: Cyst white, and of 1mm. in diameter.

Spore: With two polar capsules at one pole and the sporoplasm. Dimensions or any other characters are not given.

Remarks: Altho Nufer placed the form in the genus *Myxobolus*, this must be brought into the present group in view of the fact that the iodophilous vacuole was not detected, and that the observation is too incomplete to place it to any one of the genera.

## Gen. et spec. incert. Mavor

[Figs. 586 and 587]

1915	Mavor	1915 : 27-28, 32-33
1916	Mavor	1916 : 553-554

Habitat: Gall-bladder of *Urophycis chuss*; St. Andrews (July to September).

Vegetative form: Mavor writes as follows:

Attached, usually in large numbers, to the epithelium of the bladder, occurs a spherical or ellipsoidal trophozoite which in stained preparations is found to contain numerous nuclei. Very often clusters of *Ceratomyxa acadiensis* are found adhering to the free surface of myxosporidium. In fresh preparations the appearance is that of budding from a parent organism. An examination of sections has shown a sharp division between the myxosporidium and *Ceratomyxa acadiensis*.

Spore: Not found.

Remarks: Mavor supposed that the form under discussion probably was some species of *Myxidium* or *Chloromyxum*.

## Gen. et spec. incert. Mavor

[Figs. 588 and 589]

1916	Mavor	1916a : 68-69
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Habitat: Urinary bladder of *Stizostedion vitreum* Mitch.; Georgian Bay (Canada).

**Vegetative form:** Free forms vary greatly in shape, being rounded, elongated or branched. The largest individual  $200\mu$ . Ectoplasm layer clearly visible, sometimes projecting many bristle-like short processes. Endoplasm contains greenish granules. Trophozoites also attached to the epithelium by means of deeply stainable portion of the body.

**Spore:** Not observed.

**Remarks:** Mavor mentions resemblance of the present form to *Myxidium lieberkühni* Bütschli in many respects.

## KEYS TO THE GENERA AND SPECIES OF MYXOSPORIDIA

No key to the genera and species of Myxosporidia has been published up to the present time. This is due of course to the difficulties which accompany such an attempt. These difficulties lie chiefly in the incompleteness of the observations and descriptions of the majority of the species of Myxosporidia.

The writer has attempted in the following pages to carry out this task. The key is by no means complete, as is unavoidable in the present state of knowledge concerning this particular group of the Protozoa.

Altho the spore is the fundamental factor used in constructing this key, it was necessary to refer also to some other secondary characters such as vegetative form and habitat.

Some authors are inclined to think that the difference in host species gives an ample basis on which to record the parasite as a new species. In some cases the parasite is specific in a certain host species while in other cases a number of different host species are infected by one and the same parasite. Therefore one can not lay much emphasis upon a difference of hosts in fixing the identification of a Myxosporidian.

## KEY TO THE GENERA OF MYXOSPORIDIA

- |        |   |       |
|--------|---|-------|
| 1( 6)  | Spore approximately spherical   |       |
|        | Suborder <b>Sphaerosporea</b> Kudo 1919.....  | 2     |
| 2( 3)  | Spore with four polar capsules  |       |
|        | Family <b>CHLOROMYXIDAE</b> Thélohan 1890   |       |
|        | Genus <i>Chloromyxum</i> Mingazzini 1890.....   | (183) |
| 3( 2)  | Spore with two polar capsules   |       |
|        | Family <b>SPHAEROSPORIDAE</b> Davis 1917.....   | 4     |
| 4( 5)  | Sutural line of spore straight  |       |
|        | Genus <i>Sphaerospora</i> Thélohan 1892.....  | (185) |
| 5( 4)  | Sutural line of spore sinuous   |       |
|        | Genus <i>Sinuolinea</i> Davis 1917.....   | (186) |
| 6( 1)  | Spore not spherical.....  | 7     |
| 7(16)  | Largest diameter of spore at right angles to sutural line; two polar capsules, one on each side of sutural line                 |       |
|        | Suborder <b>Eurysporea</b> Kudo 1919  |       |
|        | Family <b>CERATOMYXIDAE</b> Doflein 1899.....   | 8     |
| 8(11)  | Shell-valves prolonged laterally.....   | 9     |
| 9(10)  | Shell-valves hemispherical or rounded   |       |
|        | Genus <i>Leptotheca</i> Thélohan 1895.....  | (179) |
| 10( 9) | Shell-valves conical; free end tapering to a more or less pointed end   |       |
|        | Genus <i>Ceratomyxa</i> Thélohan 1892.....  | (180) |
| 11( 8) | Shell-valves rather elongated; circular in cross-section.....   | 12    |
| 12(13) | Spore rounded oblong; shell longitudinally striated; polar capsules pyriform, with or without long and fine posterior filaments |       |
|        | Genus <i>Mitraspora</i> Fujita 1912 emend. Kudo 1919.....   | (183) |

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 13(12) Spore angular, not rounded..... 14
- 14(15) Spore pyramidal in front view; with its base at anterior end; with or without distinct anterior processes; shell smooth  
Genus *Myxoproteus* Doflein 1898.....(183)
- 15(14) Spore isosceles triangular in front view; anterior end attenuated; polar capsules spherical and large; shell with fine network-like ridges; with posterior fringe-like processes  
Genus *Wardia* Kudo 1919.....(183)
- 16( 7) Largest diameter of spore coincides with or at an acute angle to sutural plane; one or two polar capsules which are in sutural plane  
Suborder *Platysporea* Kudo 1919..... 17
- 17(22) Spore fusiform; two polar capsules, one at each end of spore  
Family MYXIDIDAE Thélohan 1892..... 18
- 18(21) Spore more or less regularly fusiform; shell-valves symmetrical..... 19
- 19(20) Polar filament fine and long  
Genus *Myxidium* Bütschli 1882.....(186)
- 20(19) Polar filament thick and short  
Genus *Sphaeromyxa* Thélohan 1892.....(188)
- 21(18) Spore semi-circular in front view; polar filament fine  
Genus *Zschokkella* Auerbach 1910.....(188)
- 22(17) Spore not fusiform; with one or two polar capsules at anterior extremity..... 23
- 23(26) Sporoplasm without iodophilous vacuole  
Family MYXOSOMATIDAE Poche 1913..... 24
- 24(25) Spore elongated ovoid in front view; anterior end mostly pointed  
Genus *Myxosoma* Thélohan 1892.....(189)
- 25(24) Spore more or less rounded in front view  
Genus *Lentospora* Plehn 1905.....(189)
- 26(23) Sporoplasm always with iodophilous vacuole  
Family MYXOBOLIDAE Thélohan 1892..... 27
- 27(30) Spore with posterior process; shell sometimes striated..... 28
- 28(29) Process more or less long, projecting posteriad along median line of spore; process either single or double; shell sometimes striated  
Genus *Henneguya* Thélohan 1892.....(193)
- 29(28) Process short projecting posteriad from sides; shell longitudinally striated  
Genus *Hoferellus* Berg 1898.....(173)
- 30(27) Spore without posterior process; shell unstriated; one or two polar capsules  
Genus *Myxobolus* Bütschli 1882.....(189)

## II. KEY TO THE SPECIES

### Genus LEPTOTHECA Thélohan 1895

- 1(14) Spore: sutural diameter always more than half of greatest breadth..... 2
- 2( 7) Average sutural diameter less than  $10\mu$ ..... 3
- 3( 4) Posterior margin of spore concave in front view; sutural diameter 8 to  $9\mu$ , breadth 12 to  $14\mu$ . Trophozoite usually with a long process  
*Leptotheca longipes* Auerbach 1910.....(63)
- 4( 3) Posterior margin of spore not concave..... 5
- 5( 6) Posterior margin of spore flattened; polar capsules pyriform; sutural diameter 6 to  $7\mu$ , breadth 11 to  $12\mu$ . Trophozoite with actively motile long filiform pseudopodia at rounded end  
*Leptotheca agilis* Thélohan 1892.....(60)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 6( 5) Spore regularly ovoidal; polar capsules short pyriform, opening on opposite sides; sutural diameter  $9\mu$ , breadth  $16\mu$ . Trophozoite pyriform without any recognizable pseudopodium  
*Leptotheca fusiformis* Davis 1917.....(63)
- 7( 2) Average sutural diameter of spore equal to or larger than  $10\mu$ ..... 8
- 8(13) Shell-valves symmetrically built; sutural ridge straight..... 9
- 9(10) Posterior margin of spore concave in front view; sutural diameter  $10\mu$ , breadth 18 to  $20\mu$ ; each spore formed independently  
*Leptotheca informis* Auerbach 1910.....(63)
- 10( 9) Spore regularly ovoidal..... 11
- 11(12) Trophozoite extremely polymorphous. Spore: sutural diameter 10 to  $12\mu$ , breadth 18 to  $20\mu$   
*Leptotheca polymorpha* Thélohan 1895.....(61)
- 12(11) Typical form of trophozoite elongated; anterior end depressed surrounded by short often branched pseudopodia. Spore: sutural diameter 12 to  $15\mu$ , breadth 18 to  $20\mu$   
*Leptotheca elongata* Thélohan 1895.....(60)
- 13( 8) Shell-valves asymmetrically built; sutural ridge sinuous; sutural diameter 9 to  $10\mu$ , breadth 16 to  $18\mu$ . Trophozoite rounded; movements slow  
*Leptotheca lobosa* Davis 1917.....(64)
- 14( 1) Sutural diameter equal to or less than half of greatest breadth..... 15
- 15(18) Average sutural diameter smaller than  $10\mu$ ..... 16
- 16(17) Spore arch-shaped in front view; polar capsules pyriform; sutural diameter 3 to  $4\mu$ , breadth 8 to  $10\mu$   
*Leptotheca parva* Thélohan 1895.....(61)
- 17(16) Spore cylindrical; sutural diameter  $4.5\mu$ , breadth  $9\mu$   
*Leptotheca glomerosa* Davis 1917.....(65)
- 18(15) Average sutural diameter greater than  $10\mu$ ..... 19
- 19(20) Posterior margin of spore slightly concave in front view; anterior end attenuated; polar capsules pyriform; sutural diameter  $13\mu$ , breadth  $26\mu$ . Trophozoite rounded; with active amoeboid movements  
*Leptotheca macrospora* Auerbach 1909.....(62)
- 20(19) Posterior margin of spore more or less flattened; anterior end smoothly rounded; polar capsules rounded; sutural diameter  $11\mu$ , breadth  $22\mu$ . Trophozoite elongated; pseudopodia often anastomose  
*Leptotheca scissura* Davis 1917.....(64)
- Incompletely described species  
*Leptotheca renicola* Thélohan 1895.....(61)  
*Leptotheca hepseti* Thélohan 1895.....(62)  
*Leptotheca perlata* Gurley 1894.....(62)  
*Leptotheca* sp. Awerinzew 1908.....(62)

## Genus CERATOMYXA Thélohan 1892

- 1(52) Spore constant in form and size..... 2
- 2(21) Sutural diameter equal to or less than one-eighth of total breadth..... 3
- 3(10) Sutural diameter not less than one-tenth of total breadth..... 4
- 4(9) Pseudopodia of vegetative form located at rounded end..... 5
- 5(6) Pseudopodia long filiform; with slow whiplash-like movements toward pointed extremity. Spore: sutural diameter  $12\mu$ , breadth  $118\mu$   
*Ceratomyxa flagellifera* Davis 1917.....(77)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 6( 5) Pseudopodia short lobose. . . . . 7
- 7( 8) Extremities of spore attenuated; spore large; sutural diameter 10 to 12 $\mu$ , breadth 90 to 100 $\mu$   
*Ceratomyxa sphaerulosa* Thélohan 1892. . . . . (66)
- 8( 7) Extremities of spore rounded; spore small; sutural diameter 4 $\mu$ , breadth 34 to 39 $\mu$   
*Ceratomyxa streptospora* Davis 1917. . . . . (79)
- 9( 4) Pseudopodia unlocalized; from main part of sporulating trophozoite are branched out from one to six long prolongations. Spore: sutural diameter 5 to 7 $\mu$ , breadth 50 $\mu$   
*Ceratomyxa appendiculata* Thélohan 1892. . . . . (67)
- 10( 3) Sutural diameter equal to or less than one-tenth of total breadth. . . . . 11
- 11(14) Shell-valve terminating in a fine thread-like process at distal end. . . . . 12
- 12(13) Sutural diameter 7 to 8 $\mu$ , breadth 40 to 50 $\mu$ , lateral process 250 to 300 $\mu$   
*Ceratomyxa acadensis* Mavor 1915. . . . . (71)
- 13(12) Sutural diameter 5 $\mu$ , breadth 10 to 12 $\mu$ , length of lateral process 20 $\mu$   
*Ceratomyxa linosporea* Doflein 1898. . . . . (69)
- 14(11) Shell-valves not terminating in thread-like processes. . . . . 15
- 15(20) Shell-valve drawn out into a delicate process. . . . . 16
- 16(17) Lateral process ribbon-like; sutural diameter 6 $\mu$ , breadth 140 to 150 $\mu$   
*Ceratomyxa laenia* Davis 1917. . . . . (74)
- 17(16) Lateral process not ribbon-like, but circular in cross-section. . . . . 18
- 18(19) Posterior margin of main part of spore flattened; sutural diameter 12 $\mu$ , breadth 115 to 140 $\mu$ ; trophozoite disporous  
*Ceratomyxa sphairaphora* Davis 1917. . . . . (73)
- 19(18) Posterior margin of main part of spore rounded; sutural diameter 7 $\mu$ , breadth 80 $\mu$ . Trophozoite monosporous or disporous  
*Ceratomyxa spinosa* Davis 1917. . . . . (80)
- 20(15) Shell-valve tapering gradually to attenuated point; asymmetrical; sutural diameter 9 $\mu$ , breadth 115 $\mu$   
*Ceratomyxa attenuata* Davis 1917. . . . . (75)
- 21( 2) Sutural diameter more than one-eighth of total breadth. . . . . 22
- 22(45) Sutural diameter equal to or more than one-fifth of breadth. . . . . 23
- 23(34) Shell-valves symmetrically built. . . . . 24
- 24(29) Shell-valves attenuated at distal end. . . . . 25
- 25(26) Pseudopodia peculiar network-like form. Spore: sutural diameter 12 to 20 $\mu$ , breadth 50 to 80 $\mu$   
*Ceratomyxa ramosa* Awerinzew 1907. . . . . (69)
- 26(25) Pseudopodia never unite together. . . . . 27
- 27(28) Shell-valves curved greatly posteriad; polar capsules rounded; sutural diameter 8 to 9 $\mu$ , breadth 16(?) $\mu$ . Trophozoite elongated pyriform.  
*Ceratomyxa recurvata* Davis 1917. . . . . (75)
- 28(27) Shell-valves not curved; two thickenings on posterior margin equidistant from sutural line; polar capsules pyriform; sutural diameter 40 to 45 $\mu$ , thickness 25 to 30 $\mu$ , breadth 124 to 140 $\mu$   
*Ceratomyxa tylosuri* Awerinzew 1913. . . . . (70)
- 29(24) Shell-valve rounded at distal end. . . . . 30
- 30(31) Spore arch-shaped; sutural diameter and thickness 12 to 15 $\mu$ , breadth 50 to 60 $\mu$ . Trophozoite large amoeboid.  
*Ceratomyxa spari* Awerinzew 1913. . . . . (70)
- 31(30) Spore straight. . . . . 32

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.



- 32(33) Shell-valves shorter (sutural diameter: breadth = 1:1.6)  
*Ceratomyxa coris* Georgévitch 1916.....(72)
- 33(32) Shell-valves longer (sutural diameter: breadth = 1:2.6)  
*Ceratomyxa herouardi* Georgévitch 1916.....(72)
- 34(23) Shell-valves asymmetrically built..... 35
- 35(40) Spore arch-shaped in front view..... 36
- 36(37) Sutural diameter equal to one-fifth of breadth; sutural diameter  $10\mu$ , breadth  $50\mu$   
*Ceratomyxa globulifera* Thélohan 1895.....(67)
- 37(36) Sutural diameter more than one-fifth of total breadth..... 38
- 38(39) Spore: breadth shorter; sutural diameter  $14\mu$ , breadth  $17\mu$   
*Ceratomyxa abbreviata* Davis 1917.....(76)
- 39(38) Spore: breadth longer; sutural diameter 12 to  $15\mu$ , breadth 45 to  $50\mu$   
*Ceratomyxa reticularis* Thélohan 1895.....(68)
- 40(35) Spore straight..... 41
- 41(42) Sutural diameter  $11\mu$ , breadth  $27\mu$ . Trophozoite always rounded  
*Ceratomyxa amorpha* Davis 1917.....(78)
- 42(41) Sutural diameter  $6\mu$ ..... 43
- 43(44) Trophozoite with active pseudopodia. Spore: sutural diameter  $6\mu$ , breadth 22 to  $24\mu$   
*Ceratomyxa undulata* Davis 1917.....(79)
- 44(43) Trophozoite with inactive pseudopodia. Spore: sutural diameter  $6\mu$ , breadth  $31\mu$   
*Ceratomyxa inaequalis* Doflein 1898.....(68)
- 45(22) Sutural diameter less than one-fifth of total breadth..... 46
- 46(49) Breadth of spore equal to or greater than  $50\mu$ ..... 47
- 47(48) Shell-valve tapering gradually toward distal end; sutural diameter  $8\mu$ , breadth '50 to  $56\mu$ . Trophozoite usually elongated pyriform  
*Ceratomyxa mesospora* Davis 1917.....(73)
- 48(47) Shell-valve rounded at distal end; sutural diameter 6 to  $7\mu$ , breadth  $50\mu$ . Trophozoite usually rounded or irregular form; size small  
*Ceratomyxa aggregata* Davis 1917.....(79)
- 49(46) Breadth of spore smaller than  $30\mu$ ..... 50
- 50(51) Trophozoite ordinarily spherical, diameter not exceeding 16 to  $20\mu$ ; protoplasm extremely pale looking. Spore: sutural diameter  $5\mu$ , breadth 25 to  $30\mu$ .  
*Ceratomyxa pallida* Thélohan 1895.....(67)
- 51(50) Trophozoite pyriform with a long posterior process; movements by wavelike motion of ectoplasm; also active backward movements of pseudopodia. Spore asymmetrically built; sutural diameter  $5\mu$ , breadth 24 to  $28\mu$   
*Ceratomyxa agglomerata* Davis 1917.....(77)
- 52( 1) Spore variable in size and form..... 53
- 53(54) Variation in number of shell-valves conspicuous; sutural diameter  $5\mu$ , breadth  $25\mu$   
*Ceratomyxa truncata* Thélohan 1895.....(67)
- 54(53) Variable in size and form of spore, but not in number of shell-valve..... 55
- 55(60) Trophozoite more or less definite in shape..... 56
- 56(59) Trophozoite usually pyriform..... 57
- 57(58) Trophozoite disporous. Spore: sutural diameter 7 to  $9\mu$ , breadth 15 to  $38\mu$   
*Ceratomyxa lunata* Davis 1917.....(76)
- 58(57) Trophozoite monosporous or disporous. Spore: sutural diameter 5 to  $6\mu$ , breadth 18 to  $25\mu$   
*Ceratomyxa monospora* Davis 1917.....(78)

- 59(56) Trophozoite always rounded, never pyriform. Spore: sutural diameter  $6\mu$ , breadth  $16\mu$   
*Ceratomyxa navicularia* Davis 1917.....(80)
- 60(55) Trophozoite polymorphous..... 61
- 61(62) Shell-valves symmetrically built; sutural diameter 5 to  $8\mu$ , breadth 20 to  $31\mu$   
*Ceratomyxa arcuata* Thélohan 1892.....(65)
- 62(61) Shell-valves often asymmetrically built; sutural diameter 8 to  $14\mu$ , breadth 50 to  $80\mu$   
*Ceratomyxa drepanopsettae* Awerinzew 1907.....(70)
- Incompletely described species
- Ceratomyxa* sp. (?) Awerinzew 1913.....(71)
- Ceratomyxa* sp. (?) Awerinzew 1913.....(71)
- Ceratomyxa* sp. Georgévitch 1916.....(72)

## Genus MYXOPROTEUS Doflein 1898

- 1( 2) Spore with two long ( $5\mu$ ) processes extending anteriad from sides; sutural diameter  $9\mu$ , breadth  $12\mu$   
*Myxoproteus cornutus* Davis 1917.....(82)
- 2( 1) Spore without long process..... 3
- 3( 4) Spore with two small spinous processes at anterior end; sutural diameter  $25\mu$ , breadth 18 to  $20\mu$   
*Myxoproteus ambiguus* Thélohan 1895.....(81)
- 4( 3) Spore without any process; posterior end slightly pointed; sutural diameter  $12\mu$ , breadth 10 to  $11\mu$   
*Myxoproteus cordiformis* Davis 1917.....(81)

## Genus WARDIA Kudo 1919

- 1 Spore isosceles triangular form; shell with network-like striations which end in fringe-like processes at posterior margin; sutural diameter 9 to  $10\mu$ , breadth 10 to  $12\mu$ , diameter of polar capsule  $4\mu$ .  
*Wardia ovinocua* Kudo 1919.....(82)

## Doubtfully placed species

- Wardia ohlmacheri* (Gurley 1894).....(83)

## Genus MITRASPORA Fujita 1912 emend. Kudo 1919

- 1( 4) Spore with posterior filaments..... 2
- 2( 3) Posterior filaments short (5 to  $6\mu$  long); length  $10\mu$ , breadth 8 to  $9\mu$ , thickness 6 to  $8\mu$ , polar capsule  $4\mu$  by 1.5 to  $2\mu$   
*Mitraspora cyprini* Fujita 1912.....(84)
- 3( 2) Posterior filaments of spore long (up to  $28\mu$ ); length 10 to  $11\mu$ , polar capsule 4 to  $4.5\mu$  long  
*Mitraspora caudata* Parisi 1910.....(85)
- 4( 1) Spore without posterior filament; anterior end slightly attenuated; posterior end truncate; length 15 to  $17\mu$ , breadth 5 to  $6\mu$ , thickness 4.5 to  $5.5\mu$ , polar capsule 7.5  $\mu$  by  $2\mu$   
*Mitraspora elongata* Kudo 1919.....(85)

## Genus CHLOROMYXUM Mingazzini 1890

- 1( 4) Spore with posterior appendage..... 2
- 2( 3) Posterior appendage fine and numerous; length 6 to  $9\mu$ , breadth 5 to  $6\mu$ , polar capsule 2 to  $3\mu$  by 1 to  $2\mu$   
*Chloromyxum leydi* Mingazzini 1890.....(87)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 3( 2) Posterior appendage single or bifurcated; length  $8\mu$ , breadth 6 to  $7\mu$ , appendage  $10\mu$  long  
*Chloromyxum caudatum* Thélohan 1895. . . . . (88)
- 4( 1) Spore without posterior appendage. . . . . 5
- 5(34) Spore circular or subcircular in front view; parasitic in body cavity of host. . . . . 6
- 6(29) Shell-valves marked with striations or ridges. . . . . 7
- 7(24) Main part of striations or ridges parallel to sutural line. . . . . 8
- 8(11) Shell-valves partially marked. . . . . 9
- 9(10) Ridges on each shell-valve variable in number (six found in original drawing) running closely to sutural line; diameter  $10.8\mu$   
*Chloromyxum dubium* Auerbach 1908. . . . . (91)
- 10( 9) Each shell-valve with one ridge from which eight to twelve short ones are directed toward centre of valve; oval in profile; length and breadth 8 to  $10\mu$ , thickness 5 to  $7\mu$   
*Chloromyxum trijugum* Kudo 1919. . . . . (96)
- 11( 8) Entire shell-valve marked. . . . . 12
- 12(19) Shell-valve marked with fine striations. . . . . 13
- 13(16) Spore oval in lateral view. . . . . 14
- 14(15) Trophozoite larger; size up to  $50\mu$  by  $20\mu$ ; polysporous (up to eight spores) rarely disporous. Spore: length 8 to  $9\mu$ , breadth 6 to  $7\mu$ , thickness 5 to  $6\mu$   
*Chloromyxum misgurni* Kudo 1916. . . . . (93)
- 15(14) Trophozoite smaller; size up to  $35\mu$  in diameter; polysporous (up to six spores) or disporous. Spore: length  $8\mu$ , breadth  $7\mu$ , thickness 5 to  $6\mu$   
*Chloromyxum calostomi* Kudo 1919. . . . . (98)
- 16(13) Spore circular in lateral view. . . . . 17
- 17(18) Trophozoite rounded; 40 to  $45\mu$  by 28 to  $40\mu$ . Spore: diameter 10 to  $13\mu$ , polar capsule 4 to  $6\mu$  long  
*Chloromyxum protei* Joseph 1905. . . . . (90)
- 18(17) Trophozoite irregular form; 33 to  $35\mu$  in average length. Spore: striations thicker and somewhat wavy; diameter 9 to  $9.5\mu$ , polar capsule  $3\mu$  long  
*Chloromyxum thymalli* Lebzelter 1912. . . . . (92)
- 19(12) Shell-valves marked with ridges. . . . . 20
- 20(21) Trophozoite small (average diameter of adults about  $20\mu$ ); monosporous, rarely disporous. Spore: shell-valves with ridges marked antero-posteriad; diameter 10 to  $11\mu$   
*Chloromyxum cristatum* Léger 1906. . . . . (91)
- 21(20) Trophozoite large, diameter reaching 40 to  $50\mu$ . . . . . 22
- 22(23) Ridges on shell-valves united into a line at each end and unequal in thickness; spore small; length 10 to  $12\mu$ , breadth 8 to  $10\mu$   
*Chloromyxum fujitai* Kudo 1916. . . . . (93)
- 23(22) Shell-valve with two circular and two small ridges; spore large; length  $16\mu$ , breadth  $10\mu$   
*Chloromyxum koi* Fujita 1913. . . . . (92)
- 24( 7) Striations or ridges not parallel to sutural line. . . . . 25
- 25(26) Striations irregular; posterior margin thickened at sides; diameter 7.5 to  $9\mu$   
*Chloromyxum wardi* Kudo 1919. . . . . (99)
- 26(25) Striations parallel to each other. . . . . 27
- 27(28) Striations forming acute angles with sutural line; diameter 8 to  $9\mu$   
*Chloromyxum truttiae* Léger 1906. . . . . (90)
- 28(27) Four ridges on posterior half of shell-valve converging toward anterior end; diameter  $7\mu$   
*Chloromyxum granulosum* Davis 1917. . . . . (96)

Number enclosed in parentheses refer to the page of the article on which is found the description of the species named.

29( 6)	Shell-valves without marking, beside sutural ridge . . . . .	30
30(31)	Anterior end of spore rounded; diameter 7 to 8 $\mu$ ; one or two short spinous thickenings at posterior margin <i>Chloromyxum fluviatile</i> Th��lohan 1892 . . . . .	(89)
31(30)	Anterior end of spore mucronate or truncate . . . . .	32
32(33)	Anterior end of spore mucronate; length 8 $\mu$ <i>Chloromyxum mucronatum</i> Gurley 1893 . . . . .	(89)
33(32)	Anterior end of spore truncate; spore large; length 40 to 48 $\mu$ , breadth 30 to 38 $\mu$ <i>Chloromyxum magnum</i> Awerinzew 1913 . . . . .	(92)
34( 5)	Spore rounded quadrangular in end view; conical in front view; parasitic in muscular tissue of fish . . . . .	35
35(36)	Length of spore larger than breadth; length 6 $\mu$ , breadth 5 $\mu$ <i>Chloromyxum quadratum</i> Th��lohan 1895 . . . . .	(88)
36(35)	Length (sutural diameter) of spore smaller than breadth . . . . .	37
37(38)	Spore variable in form; anterior end narrower or broader than posterior end; length 4 to 4.75 $\mu$ , breadth 5.4 to 6.5 $\mu$ <i>Chloromyxum clupei��</i> Hahn 1917 . . . . .	(94)
38(37)	Anterior end of spore drawn out; almost circular in end view; length 6 $\mu$ , breadth 7.5 $\mu$ <i>Chloromyxum funduli</i> Hahn 1915 . . . . .	(93)
Incompletely described species		
	<i>Chloromyxum diploxyi</i> Gurley 1893 . . . . .	(90)
	<i>Chloromyxum</i> sp. Awerinzew 1908 . . . . .	(91)

## Genus SPHAEROSPORA Th  lohan 1892

1( 8)	Shell-valve of spore without marking except sutural ridge . . . . .	2
2( 7)	Vegetative form amoeboid . . . . .	3
3( 4)	Movements of vegetative form active. Spore: sutural ridge fairly well marked; a pair of short filaments become visible at anterior end on warming; diameter 8 $\mu$ <i>Sphaerospora masovica</i> Cohn 1902 . . . . .	(101)
4( 3)	Vegetative form without active movements . . . . .	5
5( 6)	Spore: sutural ridge not prominent; polar capsule pyriform; diameter 8 to 13 $\mu$ , polar capsule 4 to 5 $\mu$ by 2.5 to 3.5 $\mu$ <i>Sphaerospora carassii</i> Kudo 1919 . . . . .	(103)
6( 5)	Spore: sutural ridge prominent; polar capsule spherical; slightly attenuated at anterior end; diameter 10 to 11 $\mu$ <i>Sphaerospora elegans</i> Th��lohan 1892 . . . . .	(100)
7( 2)	Vegetative form produces cyst in tissue. Spore: diameter 8 to 9 $\mu$ <i>Sphaerospora platessae</i> Woodcock 1904 . . . . .	(102)
8( 1)	Shell-valves striated . . . . .	9
9(10)	Polar capsules divergent; diameter of spore 10 to 12 $\mu$ , thickness 8 $\mu$ <i>Sphaerospora divergens</i> Th��lohan 1895 . . . . .	(100)
10( 9)	Polar capsules not divergent . . . . .	11
11(14)	Striation marked antero-posteriad . . . . .	12
12(13)	Spore with a quadrangular lamella at anterior margin; striations ending in small spines at posterior margin; length 12 to 14 $\mu$ , breadth 10 to 12 $\mu$ <i>Sphaerospora rostrata</i> Th��lohan 1895 . . . . .	(101)
13(12)	Spore smooth-contoured; polar capsules parallel to each other; diameter 7 to 10 $\mu$ <i>Sphaerospora polymorpha</i> Davis 1917 . . . . .	(102)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 14(11) Faint concentric striations; pointed at sides and middle part of posterior margin; polar capsules unequal in size; length 7 to 8 $\mu$ , breadth 6 to 7 $\mu$ , thickness 5 $\mu$   
*Sphaerospora angulata* Fujita 1912.....(102)
- Incompletely described species  
*Sphaerospora* sp. Davis 1917.....(103)  
*Sphaerospora* sp. Southwell et Prashad 1918.....(103)

## Genus SINUOLINEA Davis 1917

- 1( 4) Spore with two processes..... 2  
 2( 3) Processes lateral and long (20 $\mu$ ); spore: 9 to 11 $\mu$  long, 9 $\mu$  broad, process 18 to 22 $\mu$  long  
*Sinuolinea brachiophora* Davis 1917.....(106)
- 3( 2) Processes posteriad from sides and short; diameter 12 to 13 $\mu$ . Trophozoite opaque  
*Sinuolinea opacita* Davis 1917.....(106)
- 4( 1) Spore without process..... 5  
 5( 6) Trophozoite with active amoeboid movements. Spore: sutural ridge S-shaped at anterior part; length 15 $\mu$ , breadth 12 $\mu$ , thickness 8 $\mu$   
*Sinuolinea arborescens* Davis 1917.....(105)
- 6( 5) Trophozoite with slow amoeboid movements..... 7  
 7( 8) Sutural plane much twisted on its axis; capsulogenous cells large occupying more than half of sporal cavity; polar capsules opening on opposite sides; diameter 12 to 14 $\mu$   
*Sinuolinea capsularis* Davis 1917.....(105)
- 8( 7) Sutural plane not much twisted; diameter 15 $\mu$   
*Sinuolinea dimorpha* Davis 1916.....(104)

## Genus MYXIDIUM Bütschli 1882

- 1(16) Breadth of spore equal to or more than half of length..... 2  
 2( 7) Shell-valves unstriated..... 3  
 3( 6) Sutural plane curved into an S..... 4  
 4( 5) Spore small; length 8 to 12 $\mu$ , breadth 4 to 6 $\mu$   
*Myxidium incurvatum* Thélohan 1892.....(108)
- 5( 4) Spore large; much broader; length 20.8 to 23.4 $\mu$ , breadth 13 to 15.6 $\mu$   
*Myxidium inflatum* Auerbach 1909.....(111)
- 6( 3) Sutural plane straight; spore cylindrical; surrounded by a gelatinous envelope; length 10 to 11 $\mu$ , breadth 6 $\mu$   
*Myxidium glutinosum* Davis 1917.....(115)
- 7( 2) Shell-valves striated..... 8  
 8( 9) Sutural line curved into an S; form oval; circular in cross-section; openings of polar capsules pointed; length 11 to 13 $\mu$ , breadth 8 to 9 $\mu$   
*Myxidium oviforme* Parisi 1912.....(114)
- 9( 8) Sutural line straight..... 10  
 10(13) Sutural line coincides with longitudinal axis of spore..... 11  
 11(12) Sutural ridge distinct; extremities mucronate; length 9 to 10 $\mu$ , breadth 5 to 5.6 $\mu$ , thickness 4.75 to 5 $\mu$ . Vegetative form produces cysts, 800 to 900 $\mu$  in diameter  
*Myxidium giardi* Cépède 1906.....(110)
- 12(11) Sutural ridge faintly marked; extremities gradually drawn out; length 11 $\mu$ , breadth 8 $\mu$ . Trophozoite large and leaf-like; diameter up to 1.35 mm.  
*Myxidium phyllium* Davis 1917.....(116)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 13(10) Sutural line forming an acute angle with longitudinal axis of spore. . . . . 14
- 14(15) Shell thickened at extremities; polar capsules ovoidal; length 10 to 14 $\mu$ , breadth 6 to 8 $\mu$ , length of polar capsule 4 $\mu$   
*Myxidium striatum* Cunha et Fonseca 1917. . . . . (116)
- 15(14) Shell uniformly thick; polar capsules rounded pyriform; length 10 to 12 $\mu$ , breadth 6 $\mu$ , length of polar capsule 3 to 4 $\mu$   
*Myxidium macrocapsulare* Auerbach 1910. . . . . (113)
- 16( 1) Breadth of spore less than half of length. . . . . 17
- 17(34) Breadth more than one-third of length. . . . . 18
- 18(25) Shell-valves unstriated. . . . . 19
- 19(22) Extremities of spore pointed. . . . . 20
- 20(21) Spore: extremities sharply pointed; greatly curved; narrow; length 12 to 14 $\mu$ , breadth 5.5 to 6 $\mu$ , thickness 2.5 to 3 $\mu$   
*Myxidium depressum* Parisi 1912. . . . . (114)
- 21(20) Spore: extremities not so sharply pointed; not greatly curved; broader; length 16.2 to 19 $\mu$ , breadth 7 to 9 $\mu$   
*Myxidium bergense* Auerbach 1909. . . . . (112)
- 22(19) Extremities of spore not pointed. . . . . 23
- 23(24) Spore larger; length 15 to 20 $\mu$ , breadth 7 to 8 $\mu$   
*Myxidium sphaericum* Thélohan 1895. . . . . (109)
- 24(23) Spore smaller; length 6(?) to 14 $\mu$ , breadth 4 to 6 $\mu$ . Trophozoite mictosporous  
*Myxidium gadi* Georgévitch 1916. . . . . (115)
- 25(18) Shell-valves striated. . . . . 26
- 26(33) Spore definite in shape. . . . . 27
- 27(28) Spore constricted in middle part of length; length 15 $\mu$   
*Myxidium histophilum* Thélohan 1895. . . . . (109)
- 28(27) Spore regularly fusiform. . . . . 29
- 29(30) Vegetative form produces cyst. Spore: length 12 to 15 $\mu$ , breadth 6 $\mu$   
*Myxidium barbatulae* Cépède 1906. . . . . (110)
- 30(29) Vegetative form does not produce cyst. . . . . 31
- 31(32) Sutural line slightly curved in S-form; length 15 to 16 $\mu$ , breadth and thickness 5.5 to 6 $\mu$   
*Myxidium americanum* Kudo 1919. . . . . (117)
- 32(31) Sutural line not curved in S-shape, but bent to one side; length 15 to 18 $\mu$ , breadth and thickness 6 to 7 $\mu$   
*Myxidium kagayamai* Kudo 1919. . . . . (117)
- 33(26) Spore variable in form; straight and constricted; one side concave, the other convex; arch-shaped, etc.; length 13 to 18 $\mu$ , breadth 5.2 to 5.8 $\mu$   
*Myxidium pfeifferi* Auerbach 1908. . . . . (111)
- 34(17) Breadth of spore equal to or less than one-third of length. . . . . 35
- 35(40) Shell-valves unstriated. . . . . 36
- 36(37) Spore greatly elongated (breadth: length = 1:6.2); length 21.6 to 25.2 $\mu$ , breadth 3.6 to 4 $\mu$   
*Myxidium procerum* Auerbach 1910. . . . . (112)
- 37(36) Spore less elongated (breadth: length = 1:3 or 1:3.4). . . . . 38
- 38(39) Spore large; valves asymmetrical; length 28 $\mu$ , breadth 8 $\mu$   
*Myxidium giganteum* Doflein 1898. . . . . (110)
- 39(38) Spore small; valves symmetrical; length 12 $\mu$ , breadth 3 to 4 $\mu$   
*Myxidium danilewskyi* Laveran 1897. . . . . (109)
- 40(35) Shell-valves striated. . . . . 41
- 41(44) Spore definite in shape. . . . . 42

- 42(43) Length of polar capsule more than one-fourth of that of spore; spore 18 to 20  $\mu$  long, 5 to 6  $\mu$  broad  
*Myxidium lieberkühni* Bütschli 1882.....(107)
- 43(42) Length of polar capsule less than one-seventh of that of spore; length 16 to 17  $\mu$ , breadth 5  $\mu$   
*Myxidium mackiei* Bosanquet 1910.....(112)
- 44(41) Spore variable in shape; S-form, straight fusiform, etc.; length 9.1  $\mu$ , breadth 2.8  $\mu$ . Vegetative form produces cyst  
*Myxidium anguillae* Ishii 1915.....(114)
- Incompletely described species  
*Myxidium* sp. Gurley 1894.....(109)  
*Myxidium* sp. Awerinzew 1908.....(113)  
*Myxidium* sp. Mavor 1915.....(115)

## Genus SPHAEROMYXA Thélohan 1892

- 1( 6) Spore straight, not arch-shaped..... 2
- 2( 5) Shell-valves symmetrical..... 3
- 3( 4) Ends of spore truncate; striations longitudinal; length 15 to 20  $\mu$ , breadth 5 to 6  $\mu$ .  
*Sphaeromyxa balbianii* Thélohan 1892.....(118)
- 4( 3) Ends of spore rounded; sutural plane forming some angles with longitudinal axis of spore; striations transverse; length 12 to 14  $\mu$ , breadth 9 to 10  $\mu$   
*Sphaeromyxa immersa* Lutz 1889.....(119)
- 5( 2) Shell-valves asymmetrical; unstriated; ends less truncate; dimensions about twice or three times larger than those of *Sphaeromyxa balbianii*  
*Sphaeromyxa gasterostei* Georgévitch.....(121)
- 6( 1) Spore arch-shaped, not straight..... 7
- 7( 8) Shell-valves indistinctly striated; ends truncate; length 22 to 28  $\mu$ , breadth 3 to 4.3  $\mu$   
*Sphaeromyxa sabrazesi* Laveran et Mesnil 1900.....(120)
- 8( 7) Shell-valves unstriated..... 9
- 9(10) Spore extremely large; length 75 to 80  $\mu$ , breadth 18 to 20  $\mu$ ; ends slightly tapering  
*Sphaeromyxa exneri* Awerinzew 1913.....(121)
- 10( 9) Spore less than 35  $\mu$  in length..... 11
- 11(12) Extremities rounded; length 30 to 35  $\mu$ , breadth 8  $\mu$   
*Sphaeromyxa incurvala* Dolléin 1898.....(119)
- 12(11) Extremities truncate; sutural ridge often twisted in S-form; length 20.8 to 26  $\mu$ , breadth and thickness 5.4  $\mu$   
*Sphaeromyxa hellandi* Auerbach 1909.....(121)

## Genus ZSCHOKKELLA Auerbach 1910

- 1( 4) Shell-valves unstriated..... 2
- 2( 3) Openings of polar capsules on flattened side; spore large; length 16 to 28.8  $\mu$ , breadth 13 to 18  $\mu$   
*Zschokkella hildae* Auerbach 1910.....(122)
- 3( 2) Openings of polar capsules at pointed ends; spore small; length 11  $\mu$ , breadth 7  $\mu$   
*Zschokkella globulosa* Davis 1917.....(123)
- 4( 1) Shell-valves striated..... 5
- 5( 6) Openings of polar capsules at pointed ends; polar capsules spherical; spore larger; length 10 to 14  $\mu$ , breadth 6 to 7  $\mu$   
*Zschokkella acheilognathi* Kudo 1916.....(123)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 6( 5) Openings of polar capsules on side; polar capsules rounded pyriform; spore smaller; length 9.5 to 11.5 $\mu$ , breadth 6.5 to 7 $\mu$   
*Zschokkella nova* Klokacewa 1914.....(122)

Genus MYXOSOMA Th  lohan 1892

- 1( 2) Spore: shell thickened at anterior end; length 12 to 13 $\mu$ , breadth 7 to 8 $\mu$ , polar capsule 6 to 7 $\mu$  by 2 to 3 $\mu$ . Cysts polymorphous  
*Myxosoma dujardini* Th  lohan 1892.....(124)
- 2( 1) Spore: shell of uniform thickness and with seven to ten folds on sutural edge; length 14 $\mu$ , breadth 8 $\mu$ , thickness 6 $\mu$ , polar capsule 8 $\mu$  by 2 $\mu$ . Cysts spherical up to 360 $\mu$  in largest diameter  
*Myxosoma funduli* Kudo 1918.....(125)

Ambiguous form

- Myxosoma lobatum* Nemecek 1911.....(124)

Genus LENTOSPORA Plehn 1905

- 1( 8) Spore circular in front view..... 2
- 2( 3) Vegetative form produces cysts. Spore: length and breadth 6.3 to 7 $\mu$ , thickness 4.2 to 4.9 $\mu$   
*Lentospora dermatobia* Ishii 1916.....(127)
- 3( 2) Vegetative form does not produce cysts or cysts unobserved..... 4
- 4( 5) Spore small; trophozoites found in the blood vessel of the brain. Spore 5 to 5.5 $\mu$  in diameter.  
*Lentospora encephalina* Mulsow 1911.....(126)
- 5( 4) Spore large, greater than 7.5 $\mu$  in average diameter..... 6
- 6( 7) Spore slightly pointed at anterior end; length 8 to 10 $\mu$ , breadth 7 to 8 $\mu$ , thickness 5 to 6 $\mu$   
*Lentospora acula* Fujita 1912.....(127)
- 7( 6) Anterior end of spore rounded; diameter 6 to 10 $\mu$   
*Lentospora cerebri* Plehn 1905.....(125)
- 8( 1) Spore oval in front view..... 9
- 9(10) Spore symmetrically built; length 12 $\mu$ , breadth 9.5 $\mu$ , thickness 6 $\mu$   
*Lentospora multiplicata* Reuss 1906.....(126)
- 10( 9) Spore asymmetrically built; length 10 to 11 $\mu$ , breadth 6.5 to 7 $\mu$   
*Lentospora asymmetrica* Parisi 1912.....(126)

Genus MYXOBOLUS B  tschli 1882

- 1(18) Spore with one polar capsule..... 2
- 2( 9) Breadth of spore equal to or more than half of length..... 3
- 3( 6) Breadth of spore equal to half of length..... 4
- 4( 5) Spore larger; often calabash-shaped; anterior end drawn out into a rounded tip; shell thickened at tip; length 15 $\mu$ , breadth 7 to 8 $\mu$ , thickness 5 to 6 $\mu$   
*Myxobolus toyamai* Kudo 1915.....(131)
- 5( 4) Spore smaller; anterior end pointed; shell of uniform thickness; length 9 to 10 $\mu$ , breadth 4.5 to 5.5 $\mu$ , thickness 3 $\mu$   
*Myxobolus oculi-leucisci* Trojan 1909.....(130)
- 6( 3) Breadth of spore more than two-thirds of length..... 7
- 7( 8) Polar capsule small and oblique in position  
*Myxobolus unicapitulatus* Gurley 1893.....(129)
- 8( 7) Polar capsule long and median in position; spore broader; length 13.2 to 13.6 $\mu$ , breadth 10.1 to 10.3 $\mu$   
*Myxobolus semi* Southwell et Prashad 1918.....(132)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.



- 9( 2) Breadth of spore less than half of length..... 10
- 10(17) Breadth of spore more than two-fifths of length..... 11
- 11(16) Spore without any process..... 12
- 12(15) Shell of uniform thickness..... 13
- 13(14) Spore bent to one side; shell thickened at slightly rounded anterior tip; sutural edge without marking; length 16 to 18 $\mu$ , breadth 7 to 8 $\mu$ , polar capsule 5 to 7 $\mu$  long  
*Myxobolus piriformis* Th  lohan 1892.....(129)
- 14(13) Spore straight; shell thickened at posterior part; sutural edge with four to six markings; length 18 to 20 $\mu$ , breadth 8 $\mu$ , thickness 6 $\mu$ , polar capsule 9 to 10 $\mu$  long  
*Myxobolus fuhrmanni* Auerbach 1909.....(130)
- 15(12) Shell of uniform thickness; valves symmetrical; sutural edge with markings up to 12 in number; spore 14 to 15.5 $\mu$  long, 6 to 7.3 $\mu$  broad, 5 to 6 $\mu$  thick, polar capsule 6.3 $\mu$  by 2 to 3 $\mu$   
*Myxobolus misgurni* Kudo 1919.....(133)
- 16(11) Spore with a posterior process, 5 $\mu$  in length and as broad as spore; length 17 to 18 $\mu$ , breadth 7.5 to 8 $\mu$ , polar capsule 7 $\mu$  by 4 $\mu$   
*Myxobolus notatus* Mavor 1916.....(131)
- 17(10) Breadth of spore about one-fourth of length; spore large; polar capsule extremely large; length 30 to 32 $\mu$ , breadth 7 to 8 $\mu$ , length of polar capsule 22 to 23 $\mu$   
*Myxobolus rohila  * Southwell et Prashad 1918.....(132)
- 18( 1) Spore with two polar capsules..... 19
- 19(24) Form of spore variable..... 20
- 20(23) Spore with an intercapsular appendix at anterior end..... 21
- 21(22) Spore oval; length 10 to 12 $\mu$ , breadth 8 to 9 $\mu$ , thickness 6 $\mu$ , polar capsule 5 $\mu$  by 2 to 3 $\mu$   
*Myxobolus m  lleri* B  tschli 1882.....(128)
- 22(21) Spore pyriform or elongated oval; length 11 to 16 $\mu$ , breadth 8 to 13 $\mu$ , polar capsule 6 $\mu$  by 4 $\mu$   
*Myxobolus cycloides* Gurley 1893.....(140)
- 23(20) Spore without intercapsular appendix; circular form 7 to 8 $\mu$ , breadth 8 to 10 $\mu$ , thickness 6 $\mu$ , polar capsule 4 to 5 $\mu$  by 2 $\mu$   
*Myxobolus hylae* Johnston et Bancroft 1918.....(153)
- 24(19) Form of spore definite..... 25
- 25(28) Polar capsules in each spore regularly of considerably different size..... 26
- 26(27) Spore with an intercapsular appendix; anterior end rounded; sutural edge with folds (3 to 5); length 10 to 12 $\mu$ , breadth 8 $\mu$   
*Myxobolus dispar* Th  lohan 1895.....(135)
- 27(26) Spore without intercapsular appendix; anterior end pointed; no fold on sutural edge  
*Myxobolus inaequalis* Gurley 1893.....(135)
- 28(25) Polar capsules approximately of equal form and size..... 29
- 29(30) Sutural diameter smaller than breadth; length 6 to 7 $\mu$ , breadth 8 $\mu$   
*Myxobolus transovalis* Gurley 1893.....(139)
- 30(29) Length equal to or more than breadth of spore..... 31
- 31(102) Length longer than breadth..... 32
- 32(37) Breadth of spore less than half of length..... 33
- 33(34) Extremities of spore equally pointed; length 13 to 14.5 $\mu$ , breadth 6 to 7 $\mu$ , polar capsule 4.5 $\mu$  long  
*Myxobolus miyairii* Kudo 1919.....(155)
- 34(33) Anterior end of spore attenuated; posterior end rounded..... 35

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 35(36) Shell thickened at posterior margin; spore 12 to 15 $\mu$  long, 4 to 6.8 $\mu$  broad, polar capsule 5.5 to 7 $\mu$  by 2.1 to 2.5 $\mu$   
*Myxobolus anurus* Cohn 1895.....(142)
- 36(35) Shell of uniform thickness; spore 14.3 $\mu$  long, 6.7 $\mu$  broad, polar capsule 6.5 $\mu$  by 2 $\mu$   
*Myxobolus funduli* Kudo 1919.....(151)
- 37(32) Breadth of spore greater than half of length..... 38
- 38(41) Length of spore greater than 20 $\mu$ ..... 39
- 39(40) Spore large; subcircular and anterior end flattened in front view; sutural edge with markings; length 38 to 45 $\mu$ , breadth 32 to 38 $\mu$ , thickness 28 to 35 $\mu$ , polar capsule 15 to 17 $\mu$  long  
*Myxobolus magnus* Awerinzew 1913.....(150)
- 40(39) Spore small; extremities equally rounded; length 21 $\mu$ , breadth 15 $\mu$ , polar capsule 6 $\mu$  long  
*Myxobolus cyprini* Doflein 1898.....(143)
- 41(38) Length of spore less than 20 $\mu$ ..... 42
- 42(43) Spore with a wide (2 to 3 $\mu$ ) membraneous posterior process; length 12 $\mu$ , breadth 10 $\mu$ , length of polar capsule 4.5 $\mu$   
*Myxobolus cordis* Keysseltz 1908.....(148)
- 43(42) Normal spore without appendage..... 44
- 44(49) Breadth of sutural ridge one-third of thickness of spore..... 45
- 45(46) Length of spore smaller than 10 $\mu$ ; subcircular in front view; length 7 to 8 $\mu$ , breadth 6 to 7 $\mu$ , thickness 5 $\mu$   
*Myxobolus globosus* Gurley 1893.....(139)
- 46(45) Length of spore greater than 10 $\mu$ ..... 47
- 47(48) Spore large; elliptical in front view; with an intercapsular appendix, sutural edge with markings; length 16.9 to 21.6 $\mu$ , breadth 13 to 16.2 $\mu$ , thickness 9 $\mu$   
*Myxobolus gigas* Auerbach 1906.....(145)
- 48(47) Spore small; subcircular in front view; markings on entire sutural edge; length 10.8 to 11.7 $\mu$ , breadth 9.9 to 10.4 $\mu$ , thickness 7.2 to 9 $\mu$   
*Myxobolus aeglefini* Auerbach 1906.....(144)
- 49(44) Sutural ridge narrower..... 50
- 50(69) Spore with an intercapsular appendix..... 51
- 51(68) Intercapsular appendix triangular..... 52
- 52(57) Anterior end of spore attenuated in front view..... 53
- 53(54) Sutural edge without marking; length 11 to 12 $\mu$ , breadth 9.25 to 10.5 $\mu$   
*Myxobolus balleri* Reuss 1906.....(147)
- 54(53) Sutural edge with markings..... 55
- 55(56) Spore small; length 8 to 9.5 $\mu$ , breadth 6 to 7.5 $\mu$ , thickness 5.5 $\mu$   
*Myxobolus exiguus* Thélohan 1895.....(136)
- 56(55) Spore large; often subcircular; length 11.5 $\mu$  to 12 $\mu$ , breadth 7.5 to 8 $\mu$ , thickness 5 $\mu$   
*Myxobolus obesus* Gurley 1893.....(140)
- 57(52) Anterior end of spore broadly rounded in front view..... 58
- 58(59) Posterior portion of spore narrower; polar capsule rather large; length 11.4 to 13.5 $\mu$ , breadth 9.5 to 11 $\mu$ , thickness 8.5 to 9.5 $\mu$ , polar capsule 5.5 to 6 $\mu$  long  
*Myxobolus discrepans* Kudo 1919.....(156)
- 59(58) Extremities of spore approximately equal..... 60
- 60(61) Sutural edge without markings; spore 10 to 10.5 $\mu$  long, 8 to 8.5 $\mu$  broad, polar capsule 4.5 $\mu$  long  
*Myxobolus squamae* Keysseltz 1908.....(147)
- 61(60) Sutural edge with markings..... 62
- 62(65) Markings distinct..... 63

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 63(64) Marking variable in number along posterior margin of spore; spore more elongated; length 12 to 12.5 $\mu$ , breadth 10 to 10.5 $\mu$ , polar capsule 5.5 to 6 $\mu$  long  
*Myxobolus pfeifferi* Th  lohan 1895.....(133)
- 64(63) Sutural edge with four markings around posterior margin; spore rather short; length 11 to 12 $\mu$ , breadth 9 to 9.5 $\mu$ , thickness 4.5 to 5 $\mu$ , polar capsule 5 $\mu$  by 2.5 $\mu$   
*Myxobolus scardinii* Reuss 1906.....(146)
- 65(62) Markings indistinct..... 66
- 66(67) Markings about five at posterior margin; spore larger and shorter; length 11 to 12 $\mu$ , breadth 9.25 to 10 $\mu$ , thickness 4.5 to 5.5 $\mu$ , polar capsule 4 to 5 $\mu$  by 2.25 $\mu$   
*Myxobolus bramae* Reuss 1906.....(147)
- 67(66) Markings many along entire sutural edge except anterior tip; spore smaller, longer and thicker; length 9.25 to 10 $\mu$ , breadth 7 to 7.25 $\mu$ , thickness 5 to 5.5 $\mu$ , polar capsule 4.5 $\mu$  by 2.5 to 3 $\mu$   
*Myxobolus cyprinicola* Reuss 1906.....(147)
- 68(51) Intercapsular appendix rounded; sutural edge smooth; length 11 $\mu$ , breadth 8 $\mu$ , polar capsule 4 to 6 $\mu$  long  
*Myxobolus musculi* Keysseltz 1908.....(148)
- 69(50) Spore without intercapsular appendix..... 70
- 70(75) Length of spore less than 10 $\mu$ ..... 71
- 71(72) Spore very much flattened and small; length 6 $\mu$ , breadth 4.2 to 5 $\mu$ , polar capsule 3 $\mu$  by 2 $\mu$   
*Myxobolus minutus* Nemecek 1911.....(150)
- 72(71) Thickness of spore about half of length..... 73
- 73(74) Shell thick; length 9.25 to 10 $\mu$ , breadth 7.25 to 8.25 $\mu$ , thickness 4 to 5 $\mu$   
*Myxobolus sandrae* Reuss 1906.....(146)
- 74(73) Shell thin; spore 8.25 to 9.5 $\mu$  long, 7.25 to 8.25 $\mu$  broad, 4.5 to 5.5 $\mu$  thick  
*Myxobolus volgensis* Reuss 1906.....(145)
- 75(70) Length of spore greater than 10 $\mu$ ..... 76
- 76(85) Extremities of spore approximately equal..... 77
- 77(80) Spore elongated (breadth: length = 1:1.8 or 1:1.4)..... 78
- 78(79) Spore larger; length 14 to 17 $\mu$ , breadth 8.5 $\mu$ , thickness 5 to 6 $\mu$   
*Myxobolus oblongus* Gurley 1893.....(139)
- 79(78) Spore smaller; length 12 to 15 $\mu$ , breadth 9 to 11 $\mu$   
*Myxobolus ellipsoides* Th  lohan 1892.....(136)
- 80(77) Spore shorter (breadth: length = 1:1.3, 1:1.2 or 1:1.1)..... 81
- 81(82) Sutural edge with markings; slightly truncate at anterior end in front view; spore 9.5 to 11.5 $\mu$  long, 8.5 to 9.5 $\mu$  broad, 6.5 $\mu$  thick, polar capsule 4.75 $\mu$  by 1.5 to 2 $\mu$   
*Myxobolus mesentericus* Kudo 1919.....(157)
- 82(81) Sutural edge without markings..... 83
- 83(84) Polar capsule larger; spore 13.9 $\mu$  long, 11 $\mu$  broad, 8 $\mu$  thick  
*Myxobolus lintoni* Gurley 1893.....(138)
- 84(83) Polar capsules smaller; spore 14.5 $\mu$  long, 11.9 $\mu$  broad, polar capsule 6 $\mu$  by 3.7 $\mu$   
*Myxobolus pleuronechidae* Hahn 1917.....(152)
- 85(76) Anterior end of spore more attenuated than posterior..... 86
- 86(89) Sutural edge with markings..... 87
- 87(88) Markings five or six in number; spore 17 to 18 $\mu$  long, 10 to 13 $\mu$  broad, polar capsule 7 to 8 $\mu$   
*Myxobolus permagnus* Wegener 1910.....(149)
- 88(87) Markings sometimes present; spore 13 to 17 $\mu$  long, 8 to 10 $\mu$  broad, 5 to 7 $\mu$  thick, polar capsule 6 to 7 $\mu$  long  
*Myxobolus carassii* Klokacewa 1914.....(150)

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species

89(86)	Sutural edge without markings. . . . .	90
90(99)	Anterior end of spore highly attenuated. . . . .	91
91(96)	Length of polar capsule equal to or less than half of that of spore. . . . .	92
92(93)	Spore: anterior end pointed; length 12.4 to 13.5 $\mu$ , breadth 6.5 to 7.5 $\mu$ , thickness 5 $\mu$ , polar capsule 6 to 7 $\mu$ long. Cysts of bright golden color <i>Myxobolus aureatus</i> Ward 1919. . . . .	(154)
93(22)	Anterior tip of spore not pointed. . . . .	94
94(95)	Spore greater in thickness (6.5 to 7 $\mu$ ), length 12 to 13 $\mu$ , breadth 8.25 to 9 $\mu$ , polar capsule 6 $\mu$ by 2.5 $\mu$ ; anterior end more rounded <i>Myxobolus physophilus</i> Reuss 1906. . . . .	(146)
95(94)	Spore smaller in thickness (5.5 $\mu$ ), length 11 to 13 $\mu$ , breadth 8.25 to 9.25 $\mu$ , polar capsule 6 $\mu$ by 2.5 to 3 $\mu$ ; anterior end less rounded <i>Myxobolus macrocapsularis</i> Reuss 1906. . . . .	(146)
96(91)	Length of polar capsule greater than half of that of spore. . . . .	97
97(98)	Length of polar capsule greater than two-thirds of that of spore; spore 16 $\mu$ long, 10 to 11 $\mu$ broad, polar capsule 11 $\mu$ by 4 $\mu$ <i>Myxobolus capsulatus</i> Davis 1917. . . . .	(152)
98(97)	Length of polar capsule less than two-thirds of that of spore; spore 14 to 16 $\mu$ long, 8 to 9 $\mu$ broad, 5 to 6 $\mu$ thick, polar capsule 8 to 9 $\mu$ by 2.5 to 3 $\mu$ <i>Myxobolus koi</i> Kudo 1919. . . . .	(155)
99(90)	Anterior end of spore rounded. . . . .	100
100(101)	Cysts: size up to 1.7 mm. by 0.7 mm.; parasitic in various tissues of host. Spore 10 to 12 $\mu$ long, 9 $\mu$ broad <i>Myxobolus oviformis</i> Thélohan 1892. . . . .	(137)
101(100)	Cysts: 0.9 mm. by 0.02 mm.; parasitic in nervous system. Spore 10 to 12 $\mu$ long, 8 $\mu$ broad, 6 $\mu$ thick, polar capsule 6 to 7 $\mu$ by 2 $\mu$ <i>Myxobolus neurobius</i> Schuberg et Schröder 1905. . . . .	(144)
102(31)	Spore almost circular in front view. . . . .	103
103(104)	Anterior end somewhat attenuated; sutural edge with four markings; spore 9 to 10 $\mu$ long and broad, 6.5 to 7 $\mu$ thick, polar capsule 6 to 7.5 $\mu$ by 2.5 to 3 $\mu$ <i>Myxobolus orbiculatus</i> Kudo 1919. . . . .	(155)
104(103)	Spore regularly circular in front view. . . . .	105
105(106)	Cysts large, up to 3 mm. by 1.5 mm. Spore 10 $\mu$ long, 9.8 $\mu$ broad, 3 $\mu$ thick, polar capsule 3.8 to 5 $\mu$ long <i>Myxobolus rotundus</i> Nemeček 1911. . . . .	(149)
106(105)	Cysts small, up to 0.33 mm. in diameter. Spore 9 $\mu$ in diameter <i>Myxobolus sphaeralis</i> Gurley 1893. . . . .	(141)
Incompletely described species		
	<i>Myxobolus</i> sp. Gurley 1894. . . . .	(142)
	<i>Myxobolus</i> sp. Gurley 1894. . . . .	(142)
	<i>Myxobolus</i> sp. Gurley 1894. . . . .	(143)
	<i>Myxobolus</i> sp. Miyairi 1909. . . . .	(149)
	<i>Myxobolus</i> sp. Wegener 1910. . . . .	(149)
	<i>Myxobolus</i> sp. Lebzelter 1912. . . . .	(150)
	<i>Myxobolus</i> sp. Southwell 1915. . . . .	(151)
	<i>Myxobolus</i> sp. Kudo 1918. . . . .	(132)

## Genus HENNEGUYA Thélohan 1892

1(10)	Parasitic in urinary bladder or urinary tubule of kidney of host. . . . .	2
2( 7)	Shell-valves striated. . . . .	3

Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 3( 6) Length of tail equal to two-thirds of length of main part of spore\* ..... 4
- 4( 5) Shell-valves asymmetrical; spore smaller; total length 38 to 48 $\mu$ , length of main part 15 $\mu$ , breadth 6 to 7.5 $\mu$ , polar capsule 7.5 to 9 $\mu$  by 3 to 3.5 $\mu$ . Trophozoite disporous and polysporous  
*Henneguya gasterostei* Parisi 1912.....(169)
- 5( 4) Shell-valves symmetrical; spore broader; length of main part 13.5 to 15 $\mu$ , breadth 8 to 9 $\mu$ , thickness 6 to 7.5 $\mu$ , polar capsule 5 to 6 $\mu$  by 3 $\mu$ , length of tail 30 to 40 $\mu$ . Trophozoite mictosporous  
*Henneguya miclospora* Kudo 1919.....(173)
- 6( 3) Length of tail equal to half of length of main part of spore and single(?); length 20 to 24 $\mu$ , breadth 5 to 6 $\mu$ , length of polar capsule 4 to 5 $\mu$   
*Henneguya media* Thélohan 1892.....(161)
- 7( 2) Shell-valves unstriated..... 8
- 8( 9) Spore elongated; polar capsule longer; posterior portion of main part broad; tail wider and bifurcated to same direction; total length 19.5 to 22.5 $\mu$ , length of main part 8.5 $\mu$ , breadth 6 $\mu$ , length of tail 8 to 8.5 $\mu$   
*Henneguya légeri* Cépède 1905.....(166)
- 9( 8) Spore oval; polar capsule shorter; posterior part of main portion narrow; tail narrower and bifurcated to opposite directions; length of main part 11.5 $\mu$ , breadth 7 $\mu$ , length of tail 9.6 $\mu$ , polar capsule 3.5 $\mu$  by 2.5 $\mu$   
*Henneguya wisconsinensis* Mavor et Strasser 1916.....(170)
- 10( 1) Parasitic in tissue of host..... 11
- 11(28) Tail always appears as a single process..... 12
- 12(13) Spore small; length 4 $\mu$ , breadth 2 $\mu$   
*Henneguya tenuis* Vaney et Conte 1901.....(166)
- 13(12) Spore longer and larger, at least 27 $\mu$  long..... 14
- 14(15) Sutural edge with eight to ten markings; tail rather long; length of main part 10 to 11.5 $\mu$ , breadth 8 to 8.75 $\mu$ , thickness 4 to 5 $\mu$ , polar capsule 3 to 4 $\mu$  by 2 $\mu$ , tail up to 17 $\mu$  long  
*Henneguya brachyura* Ward 1919.....(171)
- 15(14) Sutural edge without markings..... 16
- 16(19) Total length of spore greater than 40 $\mu$ ..... 17
- 17(18) Anterior end rounded; polar capsule large; shell-valves asymmetrical; tail long; main part 10 to 11 $\mu$  long, 6 to 8 $\mu$  broad, 4 $\mu$  thick, tail 30 to 40 $\mu$  long. Cysts elongated and large up to 6 mm. by 2 mm.  
*Henneguya macrura* Gurley 1894.....(164)
- 18(17) Anterior end attenuated; polar capsule smaller; shell-valves symmetrical; tail shorter; length 20 $\mu$ , breadth 8 to 9 $\mu$ , polar capsule 8 $\mu$  by 2 to 3 $\mu$ . Cysts elongated oval and smaller, 1.1 mm. by 0.5 mm.  
*Henneguya creplini* Gurley 1894.....(162)
- 19(16) Total length of spore less than 40 $\mu$ ..... 20
- 20(21) Tail about one-third of main part; total length 38 $\mu$ , main part 26 $\mu$  long, 10 to 11 $\mu$  broad, 8 $\mu$  thick, polar capsule 11 to 14 $\mu$  by 2 to 3 $\mu$ . Cysts oval, numerous and small (130 $\mu$  by 115 $\mu$ )  
*Henneguya minuta* Cohn 1895.....(160)
- 21(20) Tail about three-sevenths of main part; total length 29 to 40 $\mu$ , main part 15 to 20 $\mu$  long, 7 to 8 $\mu$  broad, polar capsule 8 $\mu$  by 2 $\mu$ ..... 22
- 22(25) Cysts large..... 23

\*Length of main part of spore denotes in all possible cases the distance between the outer anterior tip and the posterior margin of sporal cavity; and consequently that between the latter and the distal end of the tail is the length of the tail.

<sup>†</sup> Numbers enclosed in parentheses refer to the page of the article on which is found the description of the species named.

- 23(24) Cysts spherical up to 6 mm. in diameter; parasitic in ovary  
*Henneguya oviperda* (Cohn 1895).....(160)
- 24(23) Cysts elongated up to 2 mm. by 1.5 mm.; parasitic in branchia  
*Henneguya psorospermica* Thélohan 1895.....(158)
- 25(22) Cysts rather small or size not observed..... 26
- 26(27) Elongated cysts 0.75 mm. by 0.375 mm.; parasitic in branchia  
*Henneguya leyla* (Cohn 1895).....(159)
- 27(26) Parasitic in intestinal wall  
*Henneguya peri-intestinalis* Cépède 1906.....(161)
- 28(11) Tail composed of two processes..... 29
- 29(30) Total length reaches 87.5 to 110.5 $\mu$ ; length of main part 10.5 to 15 $\mu$ , breadth  
 5 $\mu$ , length of polar capsule 5 $\mu$ , length of tail 75 to 100 $\mu$   
*Henneguya gigantea* Nemeček 1911.....(168)
- 30(29) Total length of spore less than 82 $\mu$ ..... 31
- 31(34) Sutural edge with markings..... 32
- 32(33) Tail longer and spore larger; anterior end more rounded; total length 47 $\mu$ . Cysts  
 spherical and large, up to 6 mm.  
*Henneguya salminicola* Ward 1919.....(171)
- 33(32) Tail shorter and spore smaller; anterior end slightly more attenuated; total  
 length 32 $\mu$ . Cysts lenticular, up to 2 mm. in length  
*Henneguya nüsslini* Schuberg et Schröder 1905.....(166)
- 34(31) Sutural edge without markings..... 35
- 35(38) Distal end of tail thread-like..... 36
- 36(37) Tail 40 to 50 $\mu$  in length; total length 50 to 60 $\mu$ , main part 8.5 to 9.5 $\mu$  long, 8.5 to  
 9.5 $\mu$  broad, polar capsule 4.7 to 5.5 $\mu$  by 3 $\mu$ . Cysts small, up to 50 $\mu$  in  
 diameter  
*Henneguya neapolitana* Parisi 1912.....(170)
- 37(36) Tail 10 to 30 $\mu$  in length; main part 12 $\mu$  long, 8 $\mu$  broad  
*Henneguya miyaii* Kudo 1919.....(172)
- 38(35) Distal end of tail tapers to a point and not thread-like..... 39
- 39(40) Cysts irregular in shape; size up to 2.5 mm. Spore: total length 30 to 40 $\mu$ ,  
 main part 11.5 to 15 $\mu$  long, 5 to 6.5 $\mu$  broad, polar capsule 6.5 to 8 $\mu$  by 2 to  
 2.5 $\mu$ , tail 22 to 28 $\mu$   
*Henneguya lobosa* (Cohn 1895).....(161)
- 40(39) Cysts spherical or oval..... 41
- 41(42) Anterior end of spore rounded; tail either single or double processes; total length  
 55 $\mu$ , length of main part 10 $\mu$ , breadth 7 $\mu$ , length of tail 40 to 50 $\mu$ . Cysts  
 spherical or oval up to 32 mm. by 16 mm.  
*Henneguya zschokkei* (Gurley 1893).....(165)
- 42(41) Anterior end attenuated; spore large; main part 20 to 22 $\mu$  long, breadth 8 to  
 9 $\mu$ , 6 to 7 $\mu$  thick, polar capsule 10 $\mu$  by 2 to 3 $\mu$ , tail 50 to 60 $\mu$  long  
*Henneguya acerinae* Schröder 1906.....(167)
- Incompletely described species  
*Henneguya schizura* (Gurley 1893).....(162)  
*Henneguya linearis* (Gurley 1893).....(163)  
*Henneguya gurleyi* Kudo 1893.....(163)  
*Henneguya monura* (Gurley 1893).....(164)  
*Henneguya strongylura* (Gurley 1894).....(163)  
*Henneguya kolesnikovii* (Gurley 1894).....(164)  
*Henneguya brevis* Thélohan 1895.....(162)  
*Henneguya* sp. (Gurley 1894).....(165)  
*Henneguya* sp. (Gurley 1894).....(165)  
*Henneguya* sp. Nemeček 1911.....(169)

## SUMMARY

1) All species of Myxosporidia which have been observed in various parts of the world, reaching 237 in number, are recorded with figures.

2) A new classification of Myxosporidia is proposed after discussion of those of previous authors.

3) A complete list of the specific names of the hosts that harbor Myxosporidia, is given together with the names of the organ of infection and the localities from which recorded.

4) By study of the geographical distribution of Myxosporidia, it is shown that few species are common both to American and European waters or Asiatic and European waters, while the majority of Myxosporidia are localized in definite and limited regions.

5) The study of the organal distribution of Myxosporidia in the host, shows that the gall-bladder is the organ most frequently invaded by the parasite. The kidney, branchia and urinary bladder have less chances of being attacked.

6) One new genus, *Wardia*, is established.

7) Nine new species; *Wardia ovinocua*, *Mitraspora elongata*, *Chloromyxum trijugum*, *Chloromyxum catostomi*, *Myxidium americanum*, *Myxobolus orbiculatus*, *Myxobolus discrepans*, *Myxobolus mesentericus* and *Henneguya mictospora*, are described from fresh-water fish collected in the vicinity of Urbana, Ill.

8) Six new species; *Sphaerospora carassii*, *Myxidium kagayamai*, *Myxobolus misgurni*, *Myxobolus miyairii*, *Myxobolus koi* and *Henneguya miyairii*, are recorded from fresh-water fish of Nippon.

9) One new species; *Chloromyxum wardi*, is described from Alaska. This is the second species of Myxosporidia from that part of North America.

10) Keys to the genera and species of known Myxosporidia are included.

## APPENDIX: NEW MYXOSPORIDIA FROM AUSTRALIA

The following six species described by Johnston and Bancroft did not reach the writer until the page proof was read. For this reason they could not be put in the text and are recorded here separately.

## MYXIDIUM THERAPON Johnston et Bancroft

1919 *Myxidium therapon* Johnston and Bancroft 1919 : 520-521

Habitat: In the gall bladder of *Therapon carbo* and *Th. hillii*; Thomson River at Longreach, Australia.

The parasite occurred in one specimen of the former host fish and in nine out of thirteen specimens of the latter. No visible effect of the infection on the part of the host fish was recognized.

Vegetative form: Body pale yellowish to green in color. Form(?). Size varies from 3 to 12mm. in diameter. The protoplasm is differentiated into a clear narrow ectoplasm, about  $10\mu$  in width, and a coarsely grained endoplasm. No movements could be seen on slides; but undulations were observed to travel round the margin of the trophozoite. Polysporous.

Spore: Spindle-shaped with slightly pointed extremities. Polar capsules are more or less rounded. Shell with faintly marked longitudinal striation. The sporoplasm is binucleated. Average dimensions: length 9 to  $10\mu$ , breadth  $4\mu$ , polar capsules 2 to  $3\mu$  by 1 to  $2\mu$ .

## MYXOSOMA OGILBYI Johnston et Bancroft

1919 *Myxosoma ogilbyi* Johnston and Bancroft 1919 : 521-522

Habitat: In the fibrous tissue of the gill arch of *Plectroplites ambiguus*; Thomson River at Longreach, Australia. Three out of nine host specimens examined showed the infection.

Vegetative form: The parasite forms white cysts usually close to the bases of the gill filaments. Cysts are small and rounded, being less than 1mm. in diameter. The authors simply mention that sections revealed the structure usually present in a Myxosporidian cyst.

Spore: Oval with pointed anterior end. The inner margin of the shell is indented posteriad. The sporoplasm contains a single nucleus, but not any iodophilous vacuole. Average dimensions: length 11 to  $13\mu$ , breadth 6 to  $8\mu$ , thickness  $5\mu$ , polar capsules 5 to  $6\mu$  by  $2\mu$ .

## MYXOBOLUS PLECTROPLITES Johnston et Bancroft

1919 *Myxobolus plectroplites* Johnston and Bancroft 1919 : 522-523

Habitat: In the kidney and gall-bladder of *Plectroplites ambiguus*; Thomson River at Longreach, Australia. The parasite was observed in



four out of nine host fish examined; in two cases in the kidney only, in one case only in the gall-bladder, and in one instance in both gall-bladder and kidney. Cysts were found in the kidney, while only spores were recognized in the gall-bladder.

**Vegetative form:** The cysts which could only be detected in sections, lie in the connective tissues of kidney. They are of minute size, ranging somewhat widely from  $36\mu$  in diameter to  $144$  by  $100\mu$ . According to the authors no definite structure could be found.

**Spore:** Rounded oval. It bears quite a close resemblance to that of *Myxobolus hylae* (page 153), which is slightly longer, and which has a longer polar filament than the present form. The vacuole, however, is apparently not iodophilous(?). Average dimensions: length 10 to  $12\mu$ , breadth 7 to  $8\mu$ , polar capsules 5 by  $2\mu$ , length of polar filament 30 to  $40\mu$ .

#### HENNEGUYA AUSTRALIS Johnston et Bancroft

1919 *Henneguya australis* Johnston and Bancroft 1919 : 523-524

**Habitat:** In the branchiae of *Plectroplites ambiguus*; Thomson River at Longreach, Australia. The parasite was detected in four out of nine host fish examined. The infection was extremely light in all cases.

**Vegetative form:** The parasites form cysts. They lie embedded in the spongy mass of the gill filament, and in many cases occupy a relatively large area of the section. Cysts showed two layers in section; the outermost clear ectoplasm and inner endoplasm with developing spores, the central portion of which being filled with mature spores. The spores appear to lie in a definite manner, the long axis of the spore commonly being at right angles to the boundary of the cyst, the anterior end of the spore pointing outwards.

**Spore:** Elongated ovoidal. Anterior end pointed, posterior end drawn out into a tail. The tail appears single when the spore is removed from the cyst but separates soon afterward into two halves which usually diverge widely. Two polar capsules parallel to each other are quite frequently of different length. The sporoplasm contains two nuclei and a small vacuole (iodophilous?). Average dimensions: length 11 to  $15\mu$ , breadth 3 to  $5\mu$ , thickness 3 to  $4\mu$ , polar capsules 5 to  $6\mu$  by 1 to  $2\mu$ , length of tail about  $20\mu$ .

#### HENNEGUYA GRACILIS Johnston et Bancroft

1919 *Henneguya gracilis* Johnston and Bancroft 1919 : 524-526

**Habitat:** In the gill filament of *Therapon hillii*; Thomson River at Longreach, Australia. Out of thirteen specimens examined, eight were infected. Heavy infection was recognized only in one case.

**Vegetative form:** The cyst is of definite, narrow, pear-shaped form, and lie transversely, i.e., at right angles to the long axis of the gill filament.

Spore: The spore resembles *Henneguya australis*, but is slightly smaller, while the tail is longer in proportion. The spores are arranged with long axis parallel to that of the cyst. Average dimensions: length 10 to 14 $\mu$ , breadth 2.5 to 3 $\mu$ , thickness 3 $\mu$ , polar capsules 5 to 6 $\mu$  by 1 to 2 $\mu$ , length of tail about 20 to 26 $\mu$ .

**HENNEGUYA sp. Johnston et Bancroft**

1919 *Henneguya* sp.

Johnston and Bancroft

1919 : 526

Habitat: In the branchiae of *Nematalosa elongata*; Thomson River at Longreach, Australia.

The authors state that they observed a number of spores of a *Henneguya* in the scrapings of the gill of one of four host fish.

Vegetative form: Undescribed.

Spore: Undescribed.

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### GENERAL EXPLANATION OF FIGURES

For the type species of each genus, both the vegetative form and the spore are illustrated. For the other species, except those which are new, figures of the spore are given, unless the vegetative forms are different from those of the type species or the species were reported in papers which seem to be of less universal distribution.

The original drawings were made with the Abbe drawing apparatus. The combinations used were Zeiss apochromatic objectives 16, 8, 3, and homogeneous oil immersion 2 mm. with compensation oculars 2, 4, 6, 8, 12 and 18. All the other drawings were copied from the original figures of the respective observers, an exact citation of which is given in each case, and were also made with the same drawing apparatus on the same scale except that a few figures were enlarged among those that were taken from other authors.

Magnifications were also calculated and given for those quoted figures, for which the respective authors failed to mention the scale at which the drawings were made.

## PLATE I

## EXPLANATION OF PLATE

Figs. 1 to 5. *Leptotheca agilis*.

Fig. 1. A typical trophozoite *in vivo*. After Th  lohan (1895, Fig. 29);  $\times 750$ .

Fig. 2. A young form. After Th  lohan (1895, Fig. 31).  $\times 750$ .

Fig. 3. A trophozoite in motion. After Doflein (1898, Fig. 5).

Fig. 4. A trophozoite in contracted condition. After Doflein (1898, Fig. 7).

Fig. 5. A fresh spore. After Th  lohan (1895, Fig. 30).  $\times 1500$ .

Fig. 6. A fresh mature spore of *Leptotheca elongata*. After Th  lohan (1895, Fig. 38).  $\times 1500$ .

Fig. 7. A fresh mature spore of *Leptotheca parva*. After Th  lohan (1895, Fig. 25).  $\times 1500$ .

Fig. 8. A fresh spore of *Leptotheca perlata*. After Balbiani (1884, Fig. 40).

Fig. 9. A spore of *Leptotheca macrospora*. After Auerbach (1909, Fig. 2a).  $\times 1350$ .

Fig. 10. A spore of *Leptotheca informis*, preserved in formol. After Auerbach (1910b, Fig. 1a).  $\times$  about 2000.

Fig. 11. A spore of *Leptotheca longipes*, preserved in formol. After Auerbach (1910b, Fig. 1d).  $\times$  about 2200.

Fig. 12. A fresh spore of *Leptotheca fusiformis*. After Davis (1917, Fig. 1).  $\times 1500$ .

Fig. 13. A fresh spore of *Leptotheca scissura*. After Davis (1917, Fig. 8).  $\times 1500$ .

Fig. 14. A fresh spore of *Leptotheca lobosa*. After Davis (1917, Fig. 11).  $\times 1500$ .

Fig. 15. A fresh spore of *Leptotheca glomerosa*. After Davis (1917, Fig. 13).  $\times 1500$ .

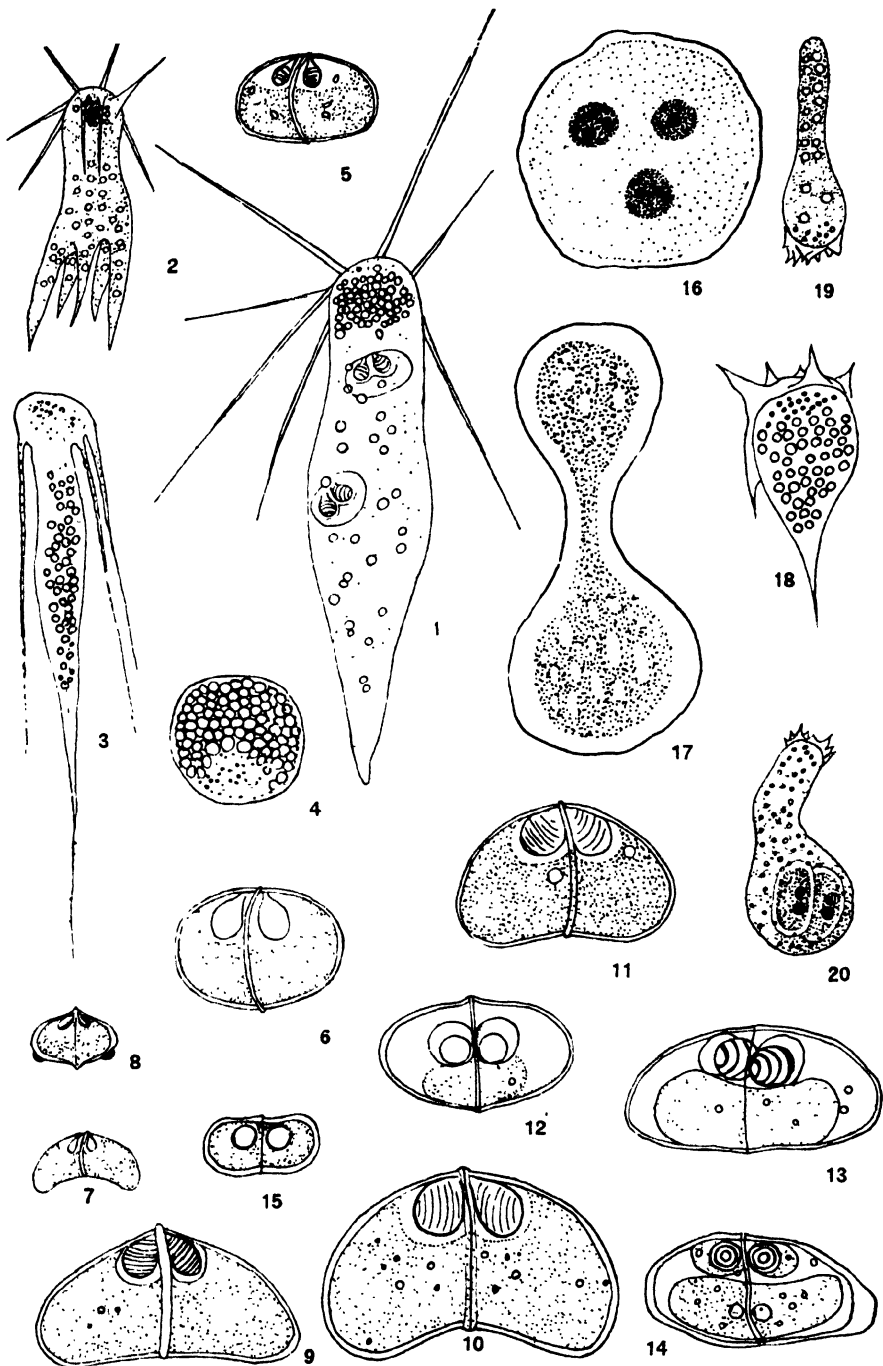
Fig. 16. A trophozoite of *Leptotheca* sp. After Awerinzew (1908, Pl. 2, Fig. 14). 1/12 and comp. oc. 12.

Fig. 17. Another trophozoite of the same. After Awerinzew (1908, Pl. 2, Fig. 17). 1/12 and comp. oc. 12.

Figs. 18 to 20. *Ceratomyxa arcuata*. After Th  lohan (1895).

Figs. 18 and 19. Typical young form. After Th  lohan (1895, Figs. 16 and 17).

Fig. 20. A trophozoite with two spores. After Th  lohan (1895, Fig. 18).



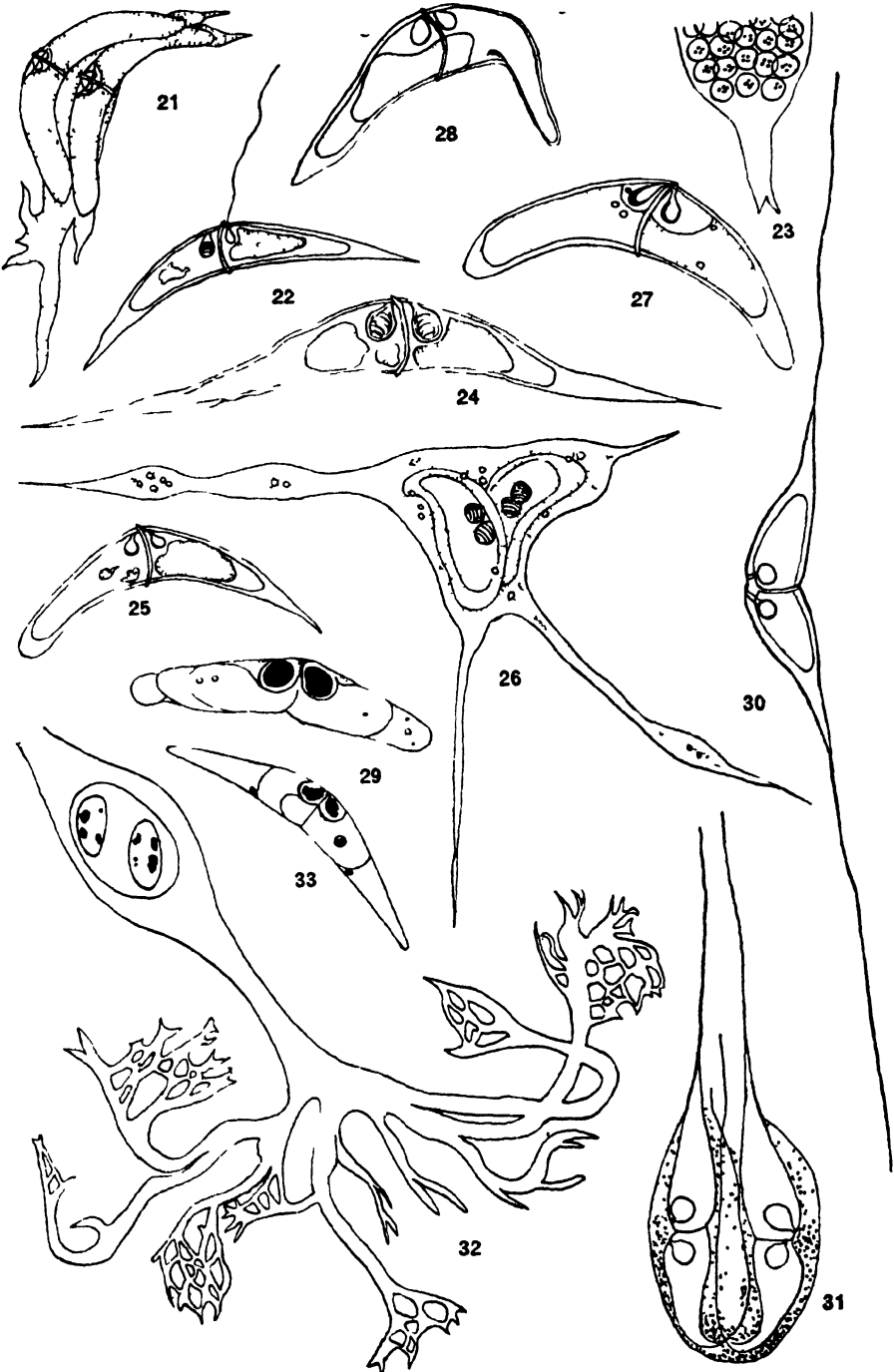




**PLATE II**

## EXPLANATION OF PLATE

- Fig. 21. A sporulating trophozoite of *Ceratomyxa arcuata*. After Parisi (1912, Fig. 6a).  
Fig. 22. A spore of *Ceratomyxa arcuata* treated with KOH. After Thélohan (1895, Fig. 19).  
×1500.  
Figs. 23 and 24. *Ceratomyxa sphaerulosa*. After Thélohan.  
Fig. 23. A part of the trophozoite (1895, Fig. 2). ×750.  
Fig. 24. A fresh spore (1895, Fig. 3). ×750.  
Fig. 25. A fresh spore of *Ceratomyxa globulifera*. After Thélohan (1895, Fig. 43). ×1500.  
Fig. 26. An adult trophozoite of *Ceratomyxa appendiculata*. After Thélohan (1895, Fig. 4).  
× about 400.  
Fig. 27. A spore of *Ceratomyxa truncata*. After Thélohan (1895, Fig. 51). ×1500.  
Fig. 28. A spore of *Ceratomyxa reticularis*. After Thélohan (1895, Fig. 27). ×1500.  
Fig. 29. A spore of *Ceratomyxa inaequalis*. After Doflein (1898, Fig. 10). ×1250.  
Figs. 30 and 31. *Ceratomyxa linotheca*. After Doflein (1898). × about 1900.  
Fig. 30. A spore (1898, Fig. 39).  
Fig. 31. A trophozoite with spores (1898, Fig. 43).  
Figs. 32 and 33. *Ceratomyxa ramosa*. After Awerinzew (1908).  
Fig. 32. A trophozoite (1908, Pl. 2, Fig. 20). Zeiss obj. D and comp. oc. 4.  
Fig. 33. A spore (1908, Pl. 2, Fig. 19). Zeiss obj. E and comp. oc. 4.





## PLATE III

## EXPLANATION OF PLATE

Figs. 34 to 39. *Ceratomyxa drepanopsettas*. Awerinzew (1908).

Fig. 34 and 35. Trophozoites (1908, Pl. 2, Figs. 7 and 9). Obj. D and oc. 4.

Fig. 36. The part of a trophozoite attached to the epithelium of the gall-bladder of the host (1908, Pl. 2, Fig. 10). Obj. E and oc. 4.

Figs. 37 to 39. Spores (1908, Pl. 1, Figs. 2, 3 and 1). Obj. D and oc. 4.

Figs. 40 and 41. Two different views of the spore of *Ceratomyxa tylosuri*. After Awerinzew (1913a, Fig. 1).  $\times$  about 350.

Figs. 42 and 43. *Ceratomyxa(?) spari*. After Awerinzew (1913a, Fig. 2).

Fig. 42. A trophozoite.

Fig. 43. A spore.  $\times$  about 345.

Figs. 44 to 47. Spores of *Ceratomyxa acadensis*. After Mavor (1916). Figs. 44 and 45 (1916, Fig. B).  $\times 270$ . Fig. 46 (1916, Fig. A)  $\times 1800$ . Fig. 47 (1916, Fig. 40)  $\times 2950$ .

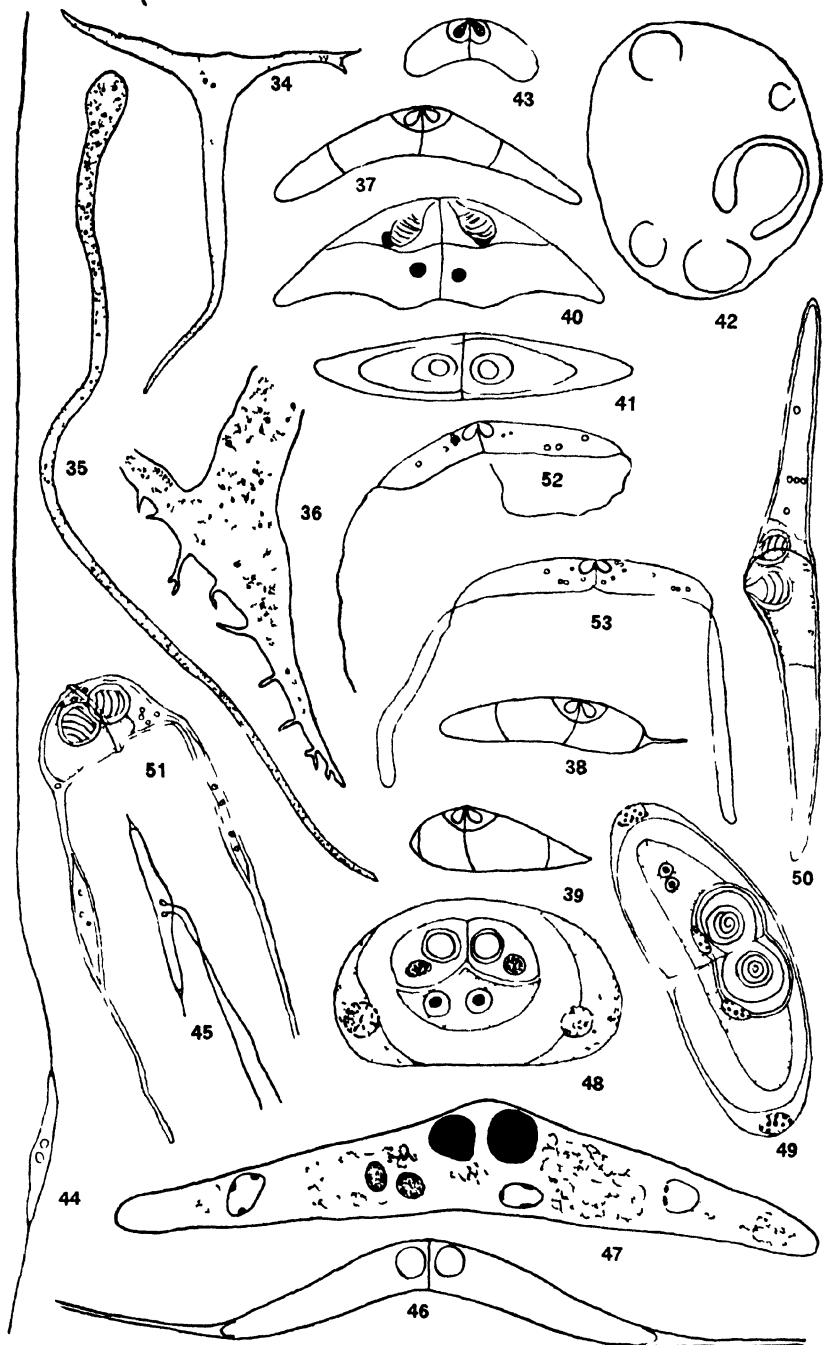
Fig. 48. A spore of *Ceratomyxa coris*. After Georgévitch (1916a, Fig. 1).

Fig. 49. A spore of *Ceratomyxa herouardi*. After Georgévitch (1917, Fig. 1).

Fig. 50. A spore of *Ceratomyxa mesospora*. After Davis (1917, Fig. 15).  $\times 1500$ .

Fig. 51. A spore of *Ceratomyxa sphairophora*. After Davis (1917, Fig. 23).  $\times 950$ .

Figs. 52 and 53. Spores of *Ceratomyxa taenia*. After Davis (1917, Figs. 26 and 25).  $\times 700$ .



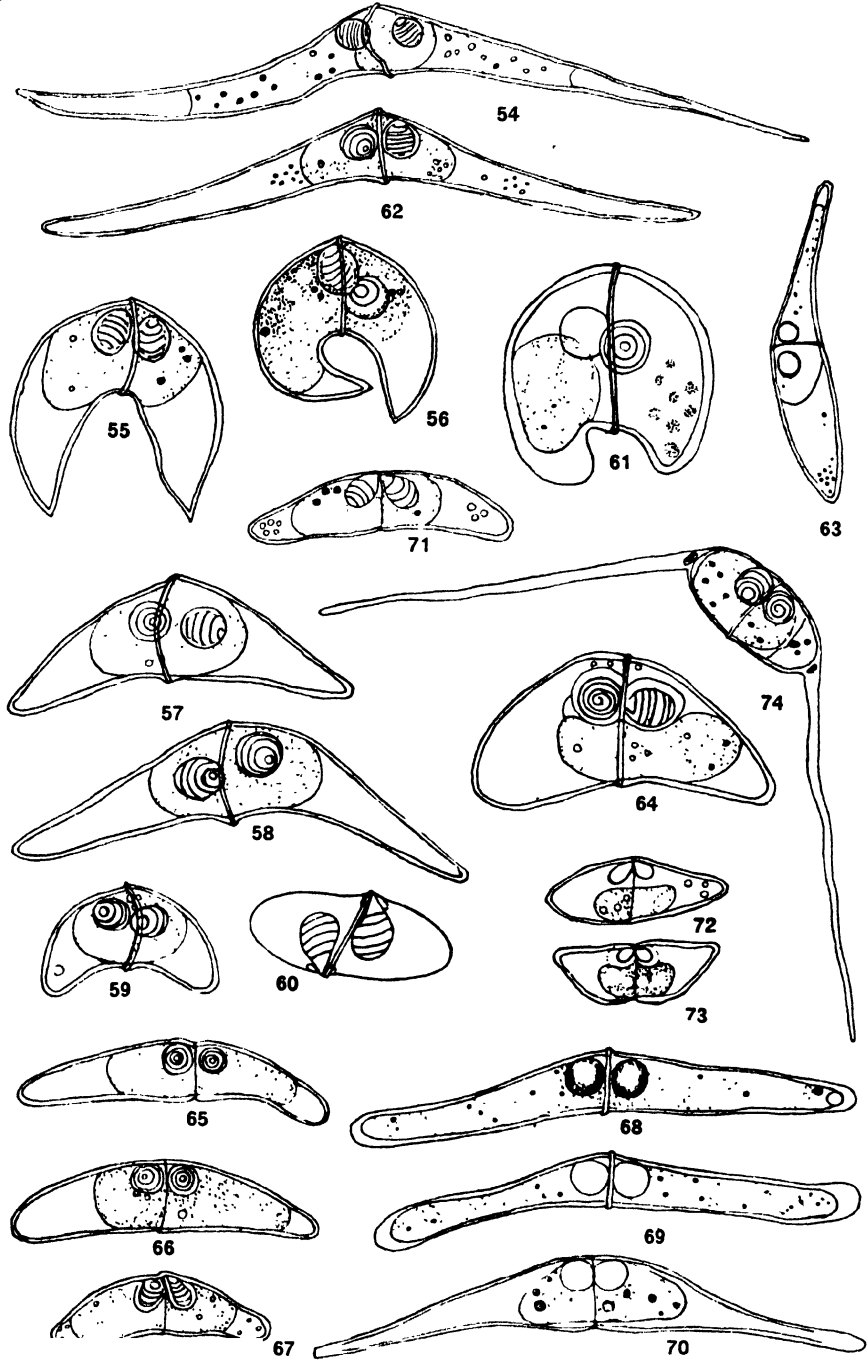




**PLATE IV**

## EXPLANATION OF PLATE

- Fig. 54. A spore of *Ceratomyxa attenuata*. After Davis (1917, Fig. 28).  $\times 950$ .
- Figs. 55 and 56. Spores of *Ceratomyxa recurvata*. After Davis (1917, Figs. 32 and 33).  $\times 1500$ .
- Figs. 57 to 60. Spores of *Ceratomyxa lunata*. After Davis (1917, Figs. 34 to 37).  $\times 1500$ .
- Fig. 61. A spore of *Ceratomyxa abbreviata*. After Davis (1917, Fig. 41).  $\times 1500$ .
- Fig. 62. A spore of *Ceratomyxa flagellifera*. After Davis (1917, Fig. 42).  $\times 1500$ .
- Fig. 63. A spore of *Ceratomyxa agglomerata*. After Davis (1917, Fig. 45).  $\times 1500$ .
- Fig. 64. A spore of *Ceratomyxa amorphica*. After Davis (1917, Fig. 47).  $\times 1500$ .
- Figs. 65 to 67. Spores of *Ceratomyxa monospora*. After Davis (1917, Figs. 57, 56 and 55).  $\times 1500$ .
- Figs. 68 and 69. Spores of *Ceratomyxa streptospora*. After Davis (1917, Figs. 59 and 60).  $\times 1500$ .
- Fig. 70. A spore of *Ceratomyxa aggregata*. After Davis (1917, Fig. 63).  $\times 1400$ .
- Fig. 71. A spore of *Ceratomyxa undulata*. After Davis (1917, Fig. 66).  $\times 1500$ .
- Figs. 72 and 73. Spores of *Ceratomyxa navicularia*. After Davis (1917, Figs. 69 and 68).  $\times 1500$ .
- Fig. 74. A spore of *Ceratomyxa spinosa*. After Davis (1917, Fig. 72).  $\times 1500$ .

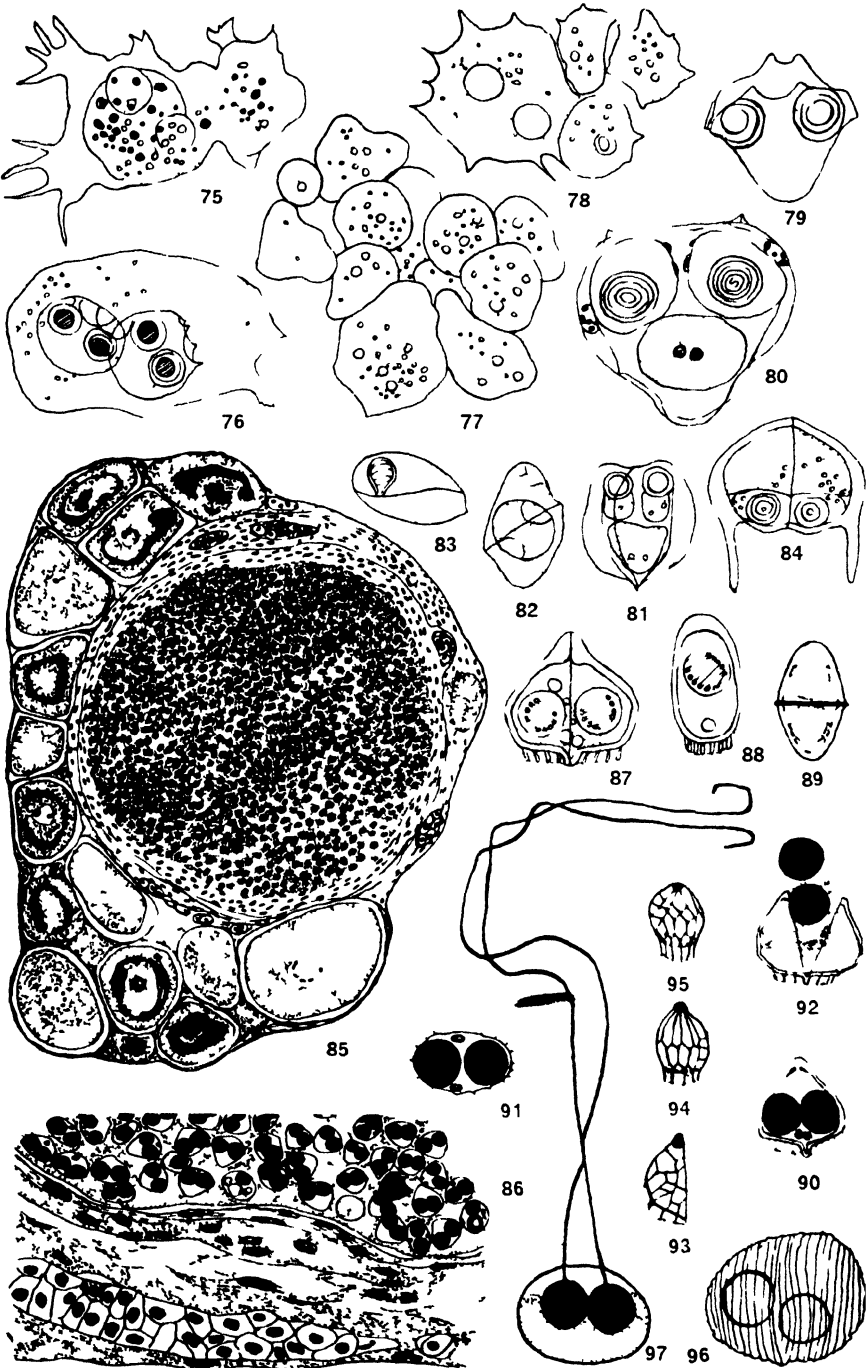




## PLATE V

## EXPLANATION OF PLATE

- Figs. 75 to 80. *Myxoproteus ambiguus*. After Doflein (1898).  
Figs. 75 and 76. Trophozoites of typical forms (1898, Figs. 12 and 52).  
Figs. 77 and 78. Young trophozoites produced by budding (1898, Figs. 55 and 56).  
Figs. 79 and 80. Spores (1898, Figs. 54 and 64).  $\times$  about 800 and 1080.  
Figs. 81 to 83. Spores of *Myxoproteus cordiformis*. After Davis (1917, Figs. 79, 80 and 78).  $\times 1500$ .  
Fig. 84. A spore of *Myxoproteus cornutus*. After Davis (1917, Fig. 85).  $\times 1400$ .  
Figs. 85 to 95. *Wardia ovinocua*. Original.  
Fig. 85. A portion of the cross-section thru an infected ovary of *Lepomis humilis*, showing the parasite in one ovum and the hypertrophied nurse cells and several connective tissue layers.  $\times 160$ .  
Fig. 86. A portion of the cross-section of a cyst.  $\times 640$ .  
Figs. 87 to 89. Three different views of fresh spore.  $\times 2000$ .  
Figs. 90 and 91. Stained spores.  $\times 1700$ .  
Fig. 92. A spore mechanically pressed and stained with Giemsa's mixture, showing the escaping polar capsules without extruding polar filament, and the sporoplasm.  $\times 1700$ .  
Figs. 93 to 95. Front and lateral views of the shell valves, exhibiting the network-like fine ridges on the surface and the posterior processes.  $\times 1700$ .  
Figs. 96 and 97. Spores of *Wardia ohlmacheri*. After Ohlmacher (1893, Figs. 4a and 2). 2mm. and oc. 4.







**PLATE VI**

## EXPLANATION OF PLATE

Figs. 98 to 104. *Mitraspora cyprini*.

Figs. 98 and 99. Trophozoites from the ureter of *Cyprinus carpio* in vivo. Original.  $\times$  about 1500.

Figs. 100 and 101. Different views of fresh spores. Original.  $\times$  about 2000.

Figs. 102 to 104. Spores. After Fujita (1912, Figs. 1a to 1c).

Figs. 105 to 107. *Mitraspora caudata*. After Parisi (1910 and 1913).

Fig. 105. A trophozoite (1910, Fig. 1).

Figs. 106 and 107. Front and lateral views of the spore (1913, Fig. 20 and 1910, Fig. 2).  $\times$  about 1600.

Figs. 108 to 113. *Chloromyxum leydigi*.

Figs. 108 and 109. Trophozoites. After Thélohan (1895, Figs. 7 and 6).  $\times 750$ .

Figs. 110 and 111. Trophozoites in division. After Doflein (1898, Figs. 57 and 58).

Figs. 112 and 113. Different views of spores. After Thélohan (1895, Figs. 10 and 9).  $\times 1500$ .

Fig. 114. A spore of *Chloromyxum caudatum*. After Thélohan (1895, Fig. 36).  $\times 1500$ .

Figs. 115 and 116. Different views of the spore of *Chloromyxum quadratum*. After Thélohan (1895, Figs. 100a and 100b).  $\times 1500$ .

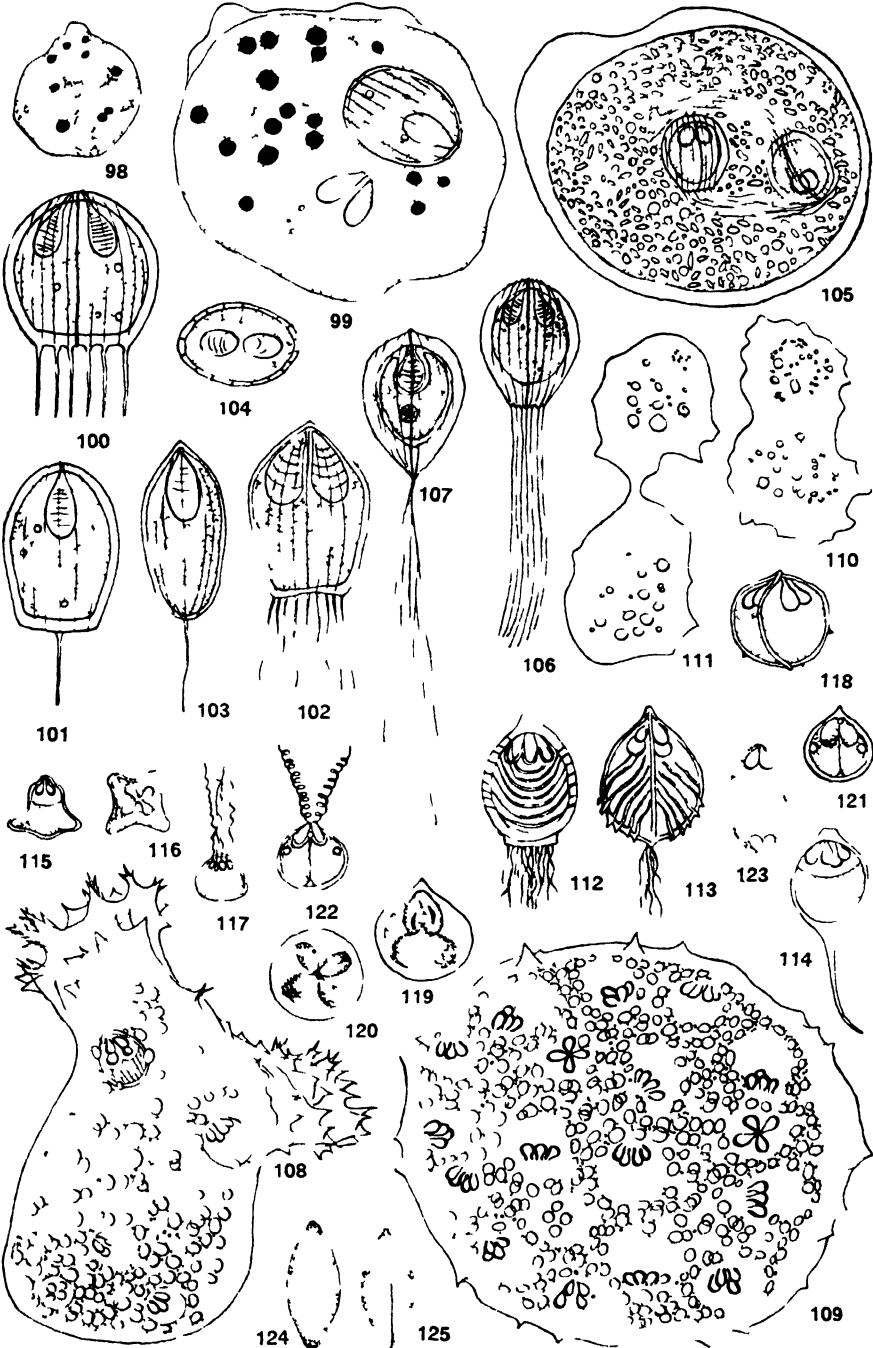
Fig. 117. A spore of *Chloromyxum quadratum* treated with nitric acid. After Thélohan (1895, Fig. 100c).  $\times 1500$ .

Fig. 118. A spore of *Chloromyxum fluviatile*. After Thélohan (1892, Fig. 2).  $\times 1500$ .

Figs. 119 and 120. Different views of the spore of *Chloromyxum mucronatum*. After Lieberkühn from Gurley (1894, Pl. 39, Fig. 5).  $\times$  about 1750.

Figs. 121 and 122. The same after Balbiani (1884, Fig. 41).  $\times$  about 1200.

Figs. 123 and 125. Spores of *Chloromyxum diplozys*. After Balbiani from Gurley (1894 Pl. 42, Figs. 13a, 13b and 13c).

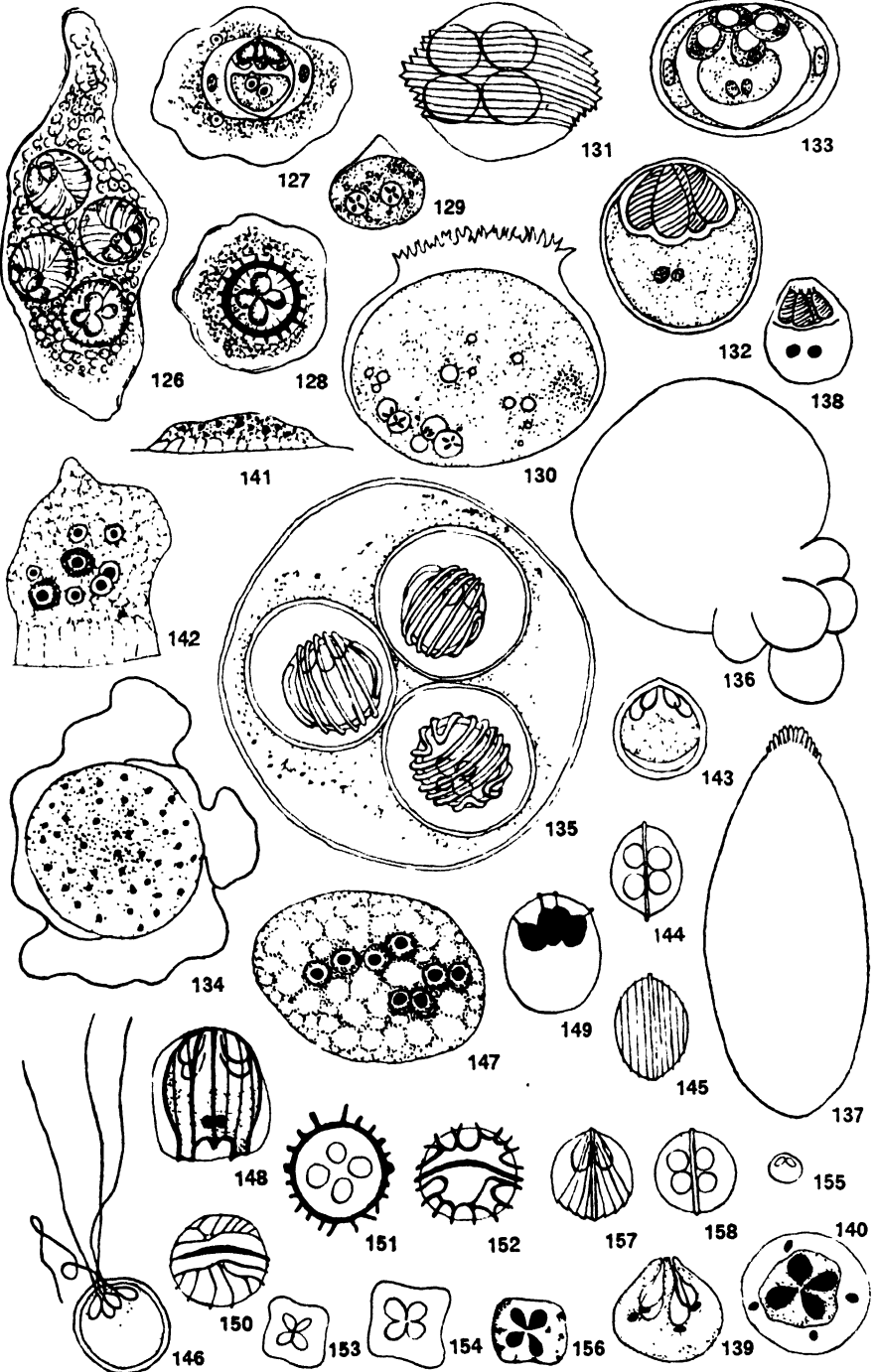




**PLATE VII**

## EXPLANATION OF PLATE

- Fig. 126. Trophozoite of *Chloromyxum truttae*. After Léger (1906, Fig. 4).  $\times 1000$ .  
Figs. 127 and 128. Trophozoites of *Chloromyxum cristatum*. After Léger (1906, Fig. 7).  $\times 1000$ .  
Figs. 129 to 133. *Chloromyxum dubium*. After Auerbach (1908).  
Figs. 129 and 130. Trophozoites (1908, Figs. 2 and 1).  
Figs. 131 and 132. Spores (1908, Figs. 3 and 4).  $\times$  about 2250.  
Fig. 133. A stained young spore (1908, Fig. 5).  
Fig. 134. Trophozoite of *Chloromyxum* sp. After Awerinzew (1908, Pl. 2: Fig. 12). Objective D and ocular 4.  
Fig. 135. *Chloromyxum koi*. After Fujita (1913).  $\times$  about 800.  
Figs. 136 to 138. *Chloromyxum magnum*. After Awerinzew (1913a, Fig. 4).  
Figs. 136 and 137. Trophozoites.  
Fig. 138. A spore.  $\times$  about 320.  
Figs. 139 and 140. Spores of *Chloromyxum funduli*. After Hahn (1915, Figs. 34 and 33).  $\times 2000$ .  
Figs. 141 to 146. *Chloromyxum misgurni*. After Kudo (1916).  $\times 1750$ .  
Figs. 141 and 142. Trophozoites (1916, Figs. 3f and 3g).  
Figs. 143 to 145. Different views of fresh spore (1916, Figs. 3a, 3c and 3b).  
Fig. 146. A spore treated with potassium hydrate (1916, Fig. 3e).  
Figs. 147 to 152. *Chloromyxum fujitai*. After Kudo (1916).  $\times 1750$ .  
Fig. 147. A trophozoite (1916, Fig. 4a).  
Fig. 148. A fresh spore (1916, Fig. 4e).  
Fig. 149. A spore stained with Giemsa's mixture (1916, Fig. 4g).  
Figs. 150 to 152. Two surface views and an optical cross-section of a stained spore, showing the ridges on the shell valves (1916, Figs. 4b, 4d and 4c).  
Figs. 153 to 156. Spores of *Chloromyxum clupeiidae*.  
Figs. 153 to 155. Fresh spores. After Linton (1901, Fig. 3). "Variously magnified."  
Fig. 156. A spore. After Hahn (1917b, Fig. 10).  $\times 1650$ .  
Figs. 157 and 158. Two views of *Chloromyxum granulosum*. After Davis (1917, Figs. 137 and 138).  $\times 1500$ .







**PLATE VIII**

## EXPLANATION OF PLATE

Figs. 159 to 182. *Chloromyxum trijugum*. Original.

Figs. 159 to 174. Trophozoites of various form and age.

Figs. 159 and 160. Trophozoites of medium size.  $\times 640$ .

Fig. 161. A trophozoite, ten minutes after it was removed from the host.  $\times 1700$ .

Figs. 162 and 163. The movements of pseudopodia of the same specimen in ten minutes  $\times 1700$ .

Fig. 164. The same specimen after thirty minutes.  $\times 1700$ .

Figs. 165 to 167. A trophozoite, showing the change of pseudopodia in five and ten minutes  $\times 1700$ .

Figs. 168 to 172. Small trophozoite with different numbers of the nuclei. Fig. 172 is probably a disporous form.  $\times 2350$ .

Fig. 173. A monosporous trophozoite with a young spore.  $\times 2350$ .

Fig. 174. A young spore.  $\times 2350$ .

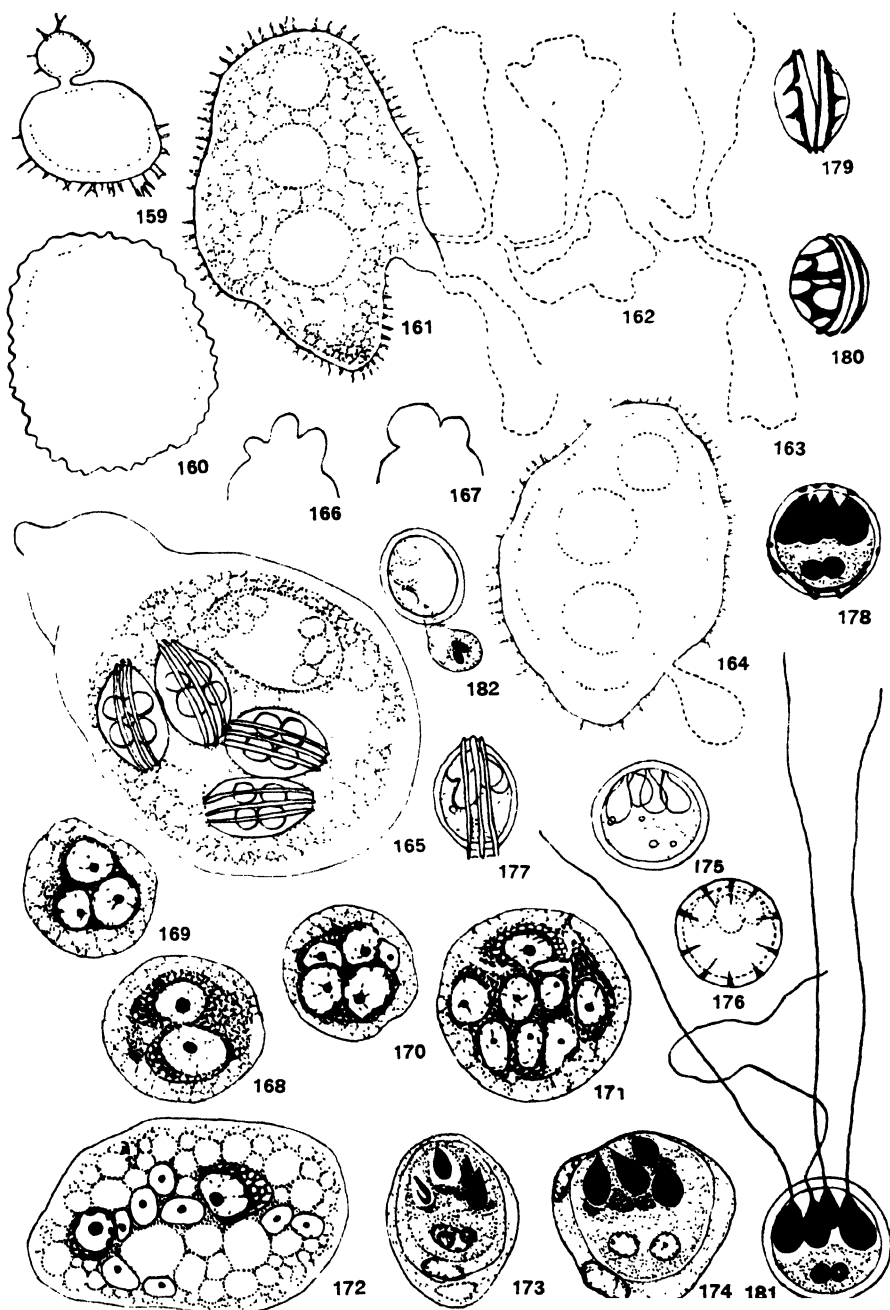
Figs. 175 to 177. Different views of fresh spores.  $\times 1700$ .

Fig. 178. A Giemsa stained spore.  $\times 1700$ .

Figs 179 and 180. Side views of the valves showing the ridges by Giemsa staining.  $\times 1700$

Fig. 181. A spore treated with potassium hydrate solution, and stained with Giemsa solution.  $\times 1700$ .

Fig. 182. A spore from which the sporoplasm is leaving the shell. From the Giemsa smear of the infected bile.  $\times 1700$ .





## PLATE IX

## EXPLANATION OF PLATE

Fig. 183 to 186. *Sphaerospora divergens*.

Fig. 183. Trophozoite. After Thélohan (1895, Fig. 12).  $\times 750$ .

Figs. 184 and 185. Two views of spore. After Auerbach (1912, Pl. 5, Fig. 4).  $\times$  about 1500.

Fig. 186. A spore treated with nitric acid. After Thélohan (1895, Fig. 13).  $\times 1500$ .

Figs. 187 and 88. Spores of *Sphaerospora elegans*. After Thélohan (1890b, Fig. 1).  $\times$  about 1000.

Fig. 189. A spore of *Sphaerospora rostrata*. After Thélohan (1895, Fig. 93).  $\times$  about 1635.

Figs. 190 to 192. Spores of *Sphaerospora masovica*. After Cohn (1902, Fig. 3).  $\times 1000$ .

Fig. 192. Spore with extruded polar filaments and "starren Fäden" by warming.

Figs. 193 and 194. Spores of *Sphaerospora plaessae*. After Woodcock (1904, Fig. 7d).  $\times 900$ .

Figs. 195 to 197. Spores of *Sphaerospora angulata*. After Fujita (1912, Fig. 3).  $\times$  about 2800.

Figs. 198 and 199. Spores of *Sphaerospora polymorpha*. After Davis (1917, Figs. 91 and 92)  $\times 1500$ .

Figs. 200 to 204. *Sphaerospora corassii*. Original.

Fig. 200. A trophozoite.  $\times 2250$ .

Figs. 201 to 203. Different views of spores.  $\times 1800$ .

Fig. 204. A young spore.  $\times 2250$ .

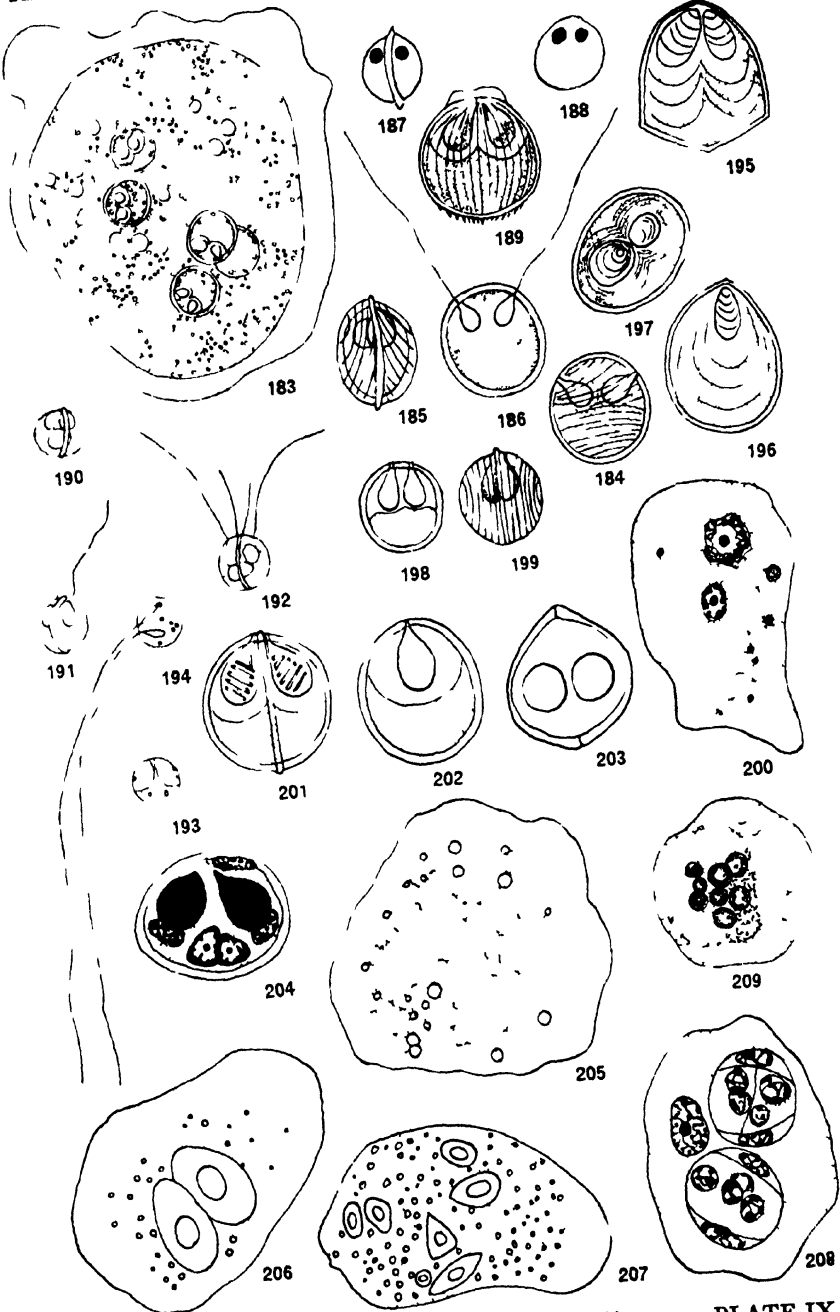
Figs. 205 to 209. *Sinuolinea dimorpha*. After Davis (1916).

Fig. 205. A fresh trophozoite (1916, Fig. 1).  $\times 1400$ .

Figs. 206 and 207. Trophozoites with erythrocytes in different stages of disintegration (1916, Figs. 2 and 57).  $\times 640$ .

Fig. 208. A stained disporous trophozoite (1916, Fig. 41).

Fig. 209. A stained gemmule (1916, Fig. 72).



KUDO

STUDIES ON MYXOSPORIDIA

PLATE IX





## PLATE X

## EXPLANATION OF PLATE

Figs. 210 to 213. *Sinuolinea dimorpha*. After Davis (1916 and 1917).

Fig. 210. A living trophozoite (1916, Fig. 56).  $\times 640$ .

Fig. 211. A living trophozoite from which a gemmule is just escaping (1916, Fig. 60).  $\times 640$ .

Figs. 212 and 213. Spores (1917, Figs. 99 and 100).  $\times 1400$ .

Figs. 214 to 216. Spores of *Sinuolinea capsularis*. After Davis (1917, Figs. 105 to 107).  $\times 1500$ .

Figs. 217 and 218. Spores of *Sinuolinea arborescens*. After Davis (1917, Figs. 109 to 110).  $\times 1500$ .

Fig. 219. Spore of *Sinuolinea opacita*. After Davis (1917, Fig. 112).  $\times 1500$ .

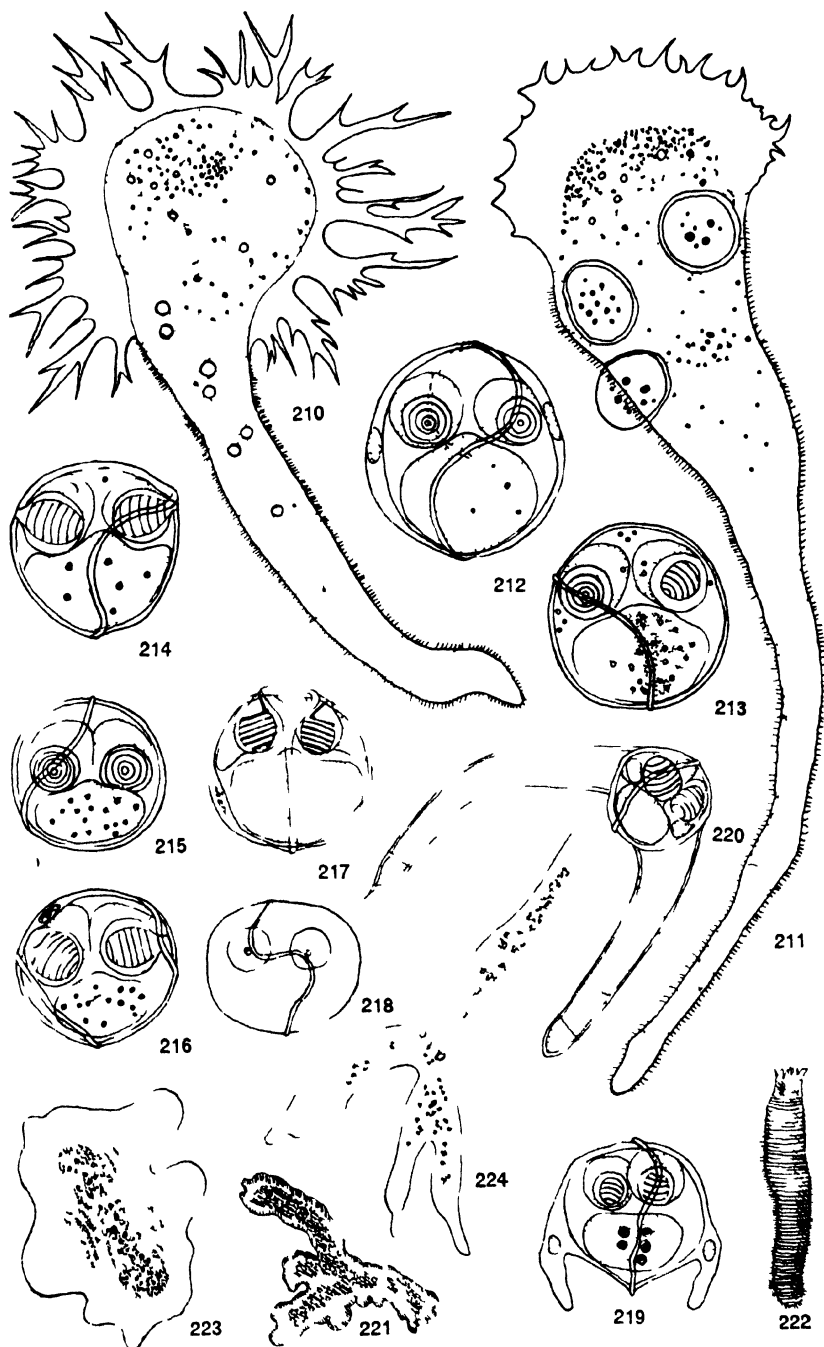
Fig. 220. Spore of *Sinuolinea brachiophora*. After Davis (1917, Fig. 113).  $\times 1500$ .

Figs. 221 to 224. *Myxidium lieberkühni*. After Bütchli (1881 and 1882).

Fig. 221. A trophozoite (1882, Pl. 38, Fig. 12).  $\times$  about 60.

Fig. 222. A trophozoite (1882, Pl. 38, Fig. 13).  $\times 160$ .

Figs. 223 and 224. Trophozoites (1881, Figs. 27 and 26).





**PLATE XI**

## EXPLANATION OF PLATE

Figs. 225 to 240. *Myxidium lieberkühni*.

Fig. 225. A trophozoite. After Lieberkühn from Gurley (1894, Pl. 43, Fig. 1a).  $\times 330$ .

Figs. 226 and 227. Trophozoites. After Bütschli (1881, Figs. 25 and 31).

Figs. 228 to 230. Stained trophozoites. After Thélohan (1895, Figs. 44, 46 and 45).  $\times 750$ .

Fig. 231. A trophozoite forming daughter individuals by budding. After Cohn (1895, Fig. 5).

Fig. 232. Four figures showing the separation of a bud. After Cohn (1895, Figs. 6a, 6b, 6d and 6e).

Fig. 233. A cross-section of a trophozoite, showing the ectoplasm, mesoplasm and endoplasm. After Cohn (1895, Fig. 2).

Fig. 234. A trophozoite. After Laveran and Mesnil (1902, Fig. 3).  $\times 500$ .

Fig. 235. A part of a trophozoite. After Laveran and Mesnil (1902, Fig. 3).  $\times 800$ .

Figs. 236 and 237. Young trophozoites undergoing division. After Laveran and Mesnil (1902, Figs. 4 and 5).  $\times 1000$ .

Fig. 238. An isolated spore. After Bütschli (1881, Fig. 32).  $\times$  about 2500.

Figs. 239 and 240. Fresh and stained spores. After Thélohan (1895, Figs. 47 and 48).  $\times 1500$ .

Figs. 241 to 251. *Myxidium incurvatum*.

Fig. 241. A monosporous trophozoite. After Parisi (1912, Fig. 1).

Fig. 242. A spore. After Thélohan (1895, Fig. 54).  $\times 1500$ .

Figs. 243 and 244. Different views of spore. After Parisi (1912, Fig. 1).

Fig. 245. A young spore. After Georgévitch (1916, Fig. 11).

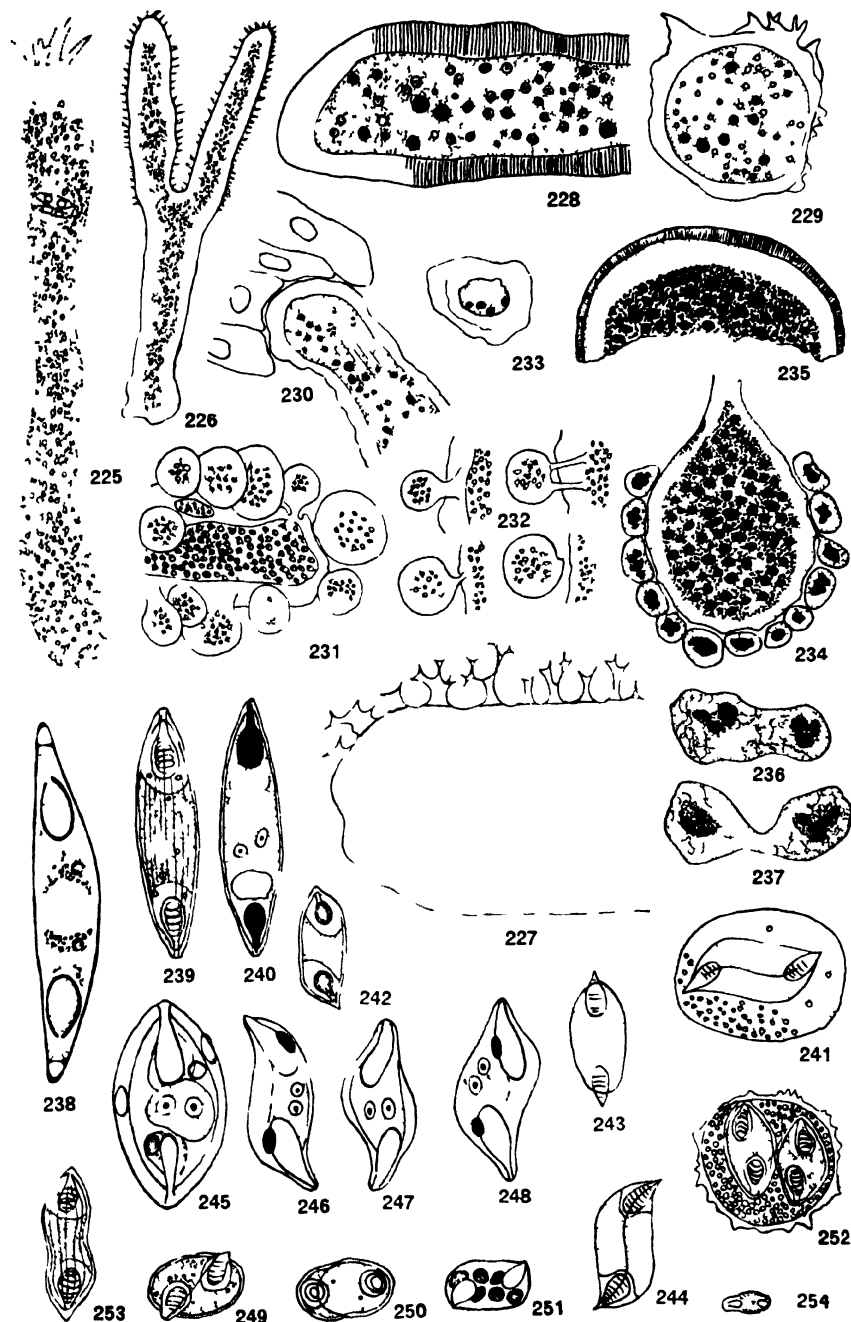
Figs. 246 to 248. Spores. After Georgévitch (1916, Figs. 10, 9 and 8).

Figs. 249 to 251. Spores. After Davis (1917, Figs. 119 to 121).  $\times 1500$ .

Fig. 252. Trophozoite of *Myxidium sphaericum*. After Thélohan (1895, Fig. 28).  $\times 1500$ .

Fig. 253. A spore of *Myxidium histophilum*. After Thélohan (1895, Fig. 49).  $\times 1500$ .

Fig. 254. A spore of *Myxidium* sp. After Leydig from Gurley (1894, Pl. 47, Fig. 6).







## PLATE XII

## EXPLANATION OF PLATE

Figs. 255 to 257. *Myxidium danilewskyi*. After Laveran (1898).

Figs. 255 and 256. Longitudinal and transverse sections thru renal tubules, showing the trophozoites (1898, Figs. 1 and 2). Fig. 255.  $\times 350$ .

Fig. 257. Spores (1898, Figs. 4, 5 and 6).  $\times 800$ .

Fig. 258. Spores of *Myxidium giganteum*. After Doflein (1898, Fig. 48).  $\times$  about 500.

Figs. 259 to 261. Spores of *Myxidium giardi*. After Cépède (1906a, Figs. 1, 3 and 2).  $\times 2000$ .

Figs. 262 to 265. Spores of *Myxidium pfeifferi*. After Auerbach (1908, Figs. 6 and 7).  $\times$  about 2000, except Fig. 265.

Fig. 266. A spore of *Myxidium inflatum*. After Auerbach (1909, Fig. 3a).  $\times$  about 1500.

Fig. 267. A spore of *Myxidium bergense*. After Auerbach (1910a, Fig. 57).  $\times$  about 1820.

Fig. 268. A spore of *Myxidium procerum*. After Auerbach (1910a, Fig. 58).  $\times$  about 2000.

Figs. 269 to 271. Spores of *Myxidium mackiei*. After Bosanquet (1910, Fig. 12).  $\times$  about 1250.

Figs. 272 and 273. Spores of *Myxidium macrocapsulare*. After Auerbach (1910d, Figs. 1a and 1b).  $\times 3000$ .

Figs. 274 to 276. *Myxidium* sp. After Awerinzew (1908 and 1911).

Fig. 274. A monosporous trophozoite (1911, Fig. C).

Fig. 275. A disporous trophozoite (1908, Pl. 2, Fig. 6). Obj. E and oc. 4.

Fig. 276. A spore (1908, Pl. 1a, Fig. 17).  $\times$  about 1000.

Figs. 277 and 278. Spores of *Myxidium depressum*. After Parisi (1912, Figs. 2a and 2b).  $\times$  about 1600.

Figs. 279 and 280. Spores of *Myxidium oviforme*. After Parisi (1912, Fig. 3).  $\times$  about 1600.

Figs. 281 to 284. Spores of *Myxidium anguillae*. After Ishii (1915, Fig. 3a).  $\times 1450$ .

Figs. 285 and 286. *Myxidium* sp. After Mavor (1915).

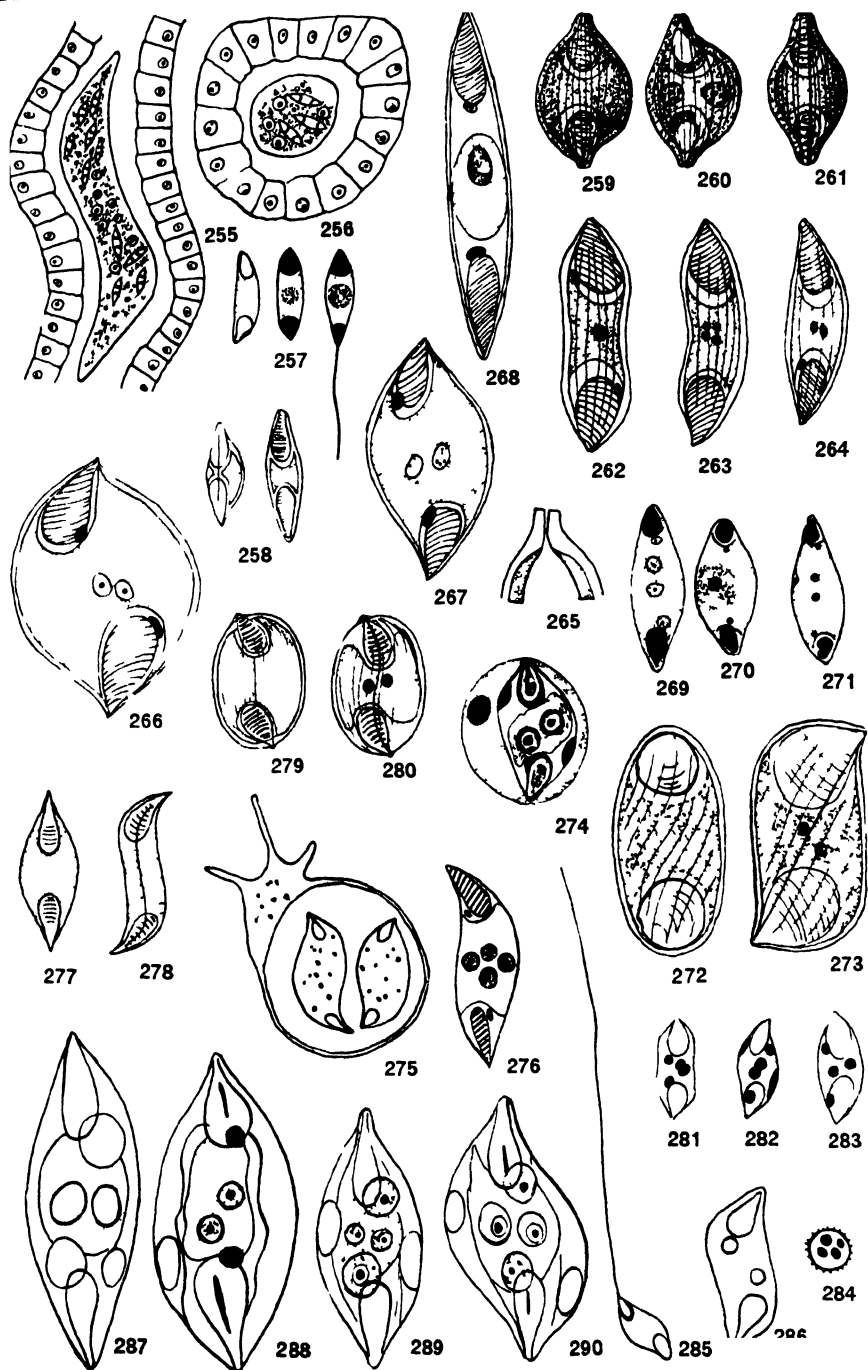
Fig. 285. A spore treated with ammonia water (1915, Fig. 3a).  $\times 660$ .

Fig. 286. A spore (1915, Fig. 3b).  $\times 1320$ .

Figs. 287 to 290. Spores of *Myxidium gadi*. After Georgévitch (1916, Figs. 1, 4, 3 and 2).

Fig. 228. A spore from *Solea vulgaris*.

Figs. 289 and 290. Young spores.

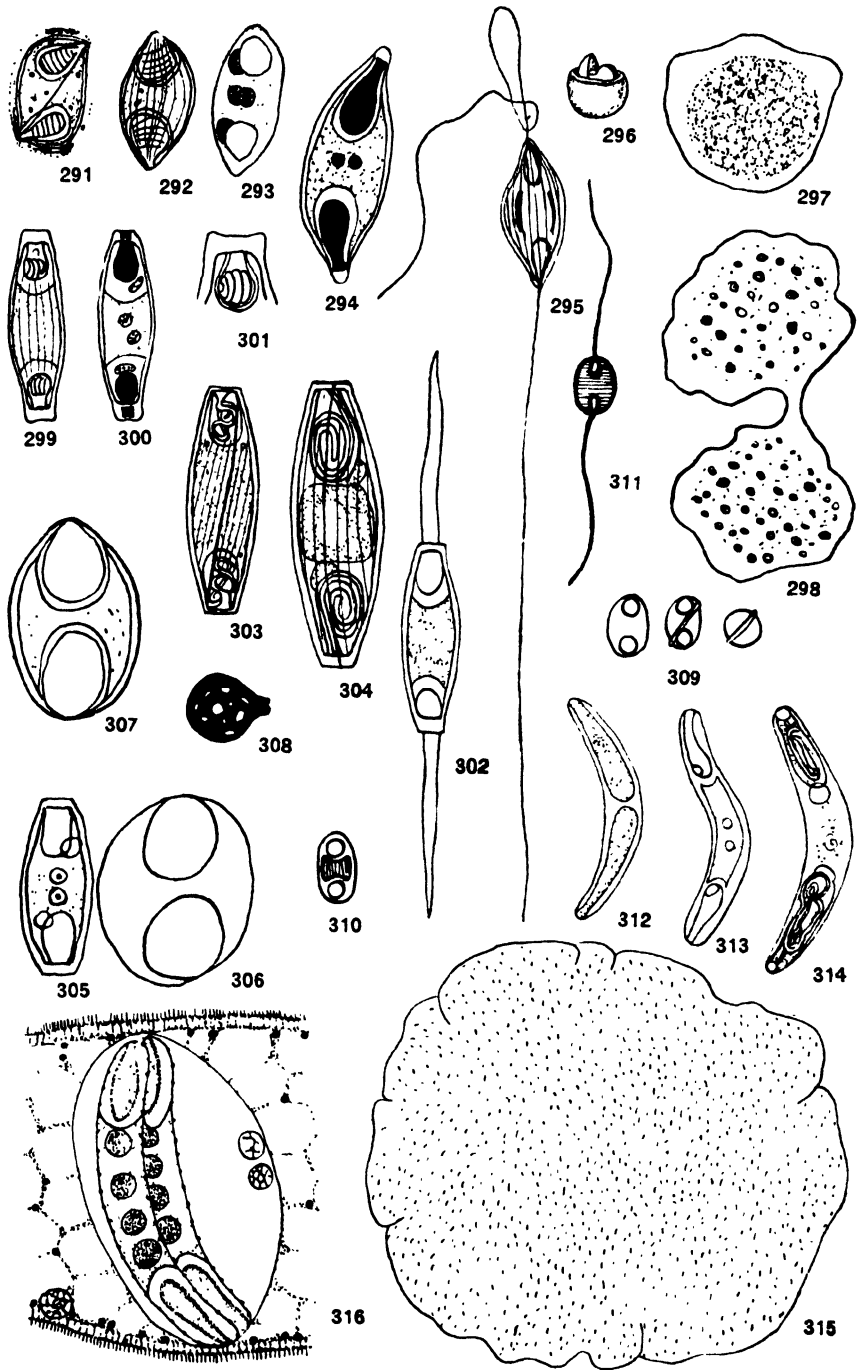




**PLATE XIII**

## EXPLANATION OF PLATE

- Fig. 291. A spore of *Myxidium glutinosum*. After Davis (1917, Fig. 124).  $\times 1400$ .  
Figs. 292 and 293. Spores of *Myxidium phyllium*. After Davis (1917, Figs. 126 and 127).  $\times 2000$ .  
Figs. 294 and 295. Spores of *Myxidium kagayamai*. After Kudo (1916, Fig. 2).  $\times 1750$  and  $\times 1000$  respectively.  
Figs. 296 to 307. *Sphaeromyxa balbianii*.  
Fig. 296. A trophozoite. After Thélohan (1895, Fig. 57).  $\times 3$ .  
Fig. 297. A trophozoite. After Davis (1917, Fig. 128).  $\times 640$ .  
Fig. 298. A trophozoite in plasmotomy. After Georgévitch (1916, Fig. 15).  
Figs. 299 and 300. Spores. After Thélohan (1895, Figs. 58 and 59).  $\times 1500$ .  
Fig. 301. An end of a spore. After Thélohan (1895, Fig. 60).  
Fig. 302. A spore treated with nitric acid. After Thélohan (1895, Fig. 61).  
Fig. 303. A spore. After Parisi (1912, Fig. 4).  $\times$  about 1750.  
Fig. 304. A spore. After Davis (1917, Fig. 130).  $\times 2100$ .  
Figs. 305 to 307. Mature and young spores (Figs. 306 and 307). After Georgévitch (1916, Figs. 17, 20 and 19).  
Figs. 308 to 311. *Sphaeromyxa immersa*. After Lutz (1889: 301).  
Fig. 308. An infected gall-bladder of *Bufo aqua* (1889, Fig. 1).  $\times 1$ .  
Fig. 309. Spores (1889, Figs. 4, 5 and 6).  
Fig. 310. A spore (1889, Fig. 10).  $\times 600$ .  
Fig. 311. A spore with extruded polar filaments (1889, Fig. 7).  
Figs. 312 to 314. Spores of *Sphaeromyxa incurvata*. After Doflein (1898, Fig. 49).  $\times$  about 1000.  
Figs. 315 and 316. *Sphaeromyxa sabrazesi*. After Schröder (1907).  
Fig. 315. A trophozoite (1907, Fig. 1).  $\times 15$ .  
Fig. 316. A cross section thru a trophozoite (1907, Fig. 3).  $\times 1500$ .



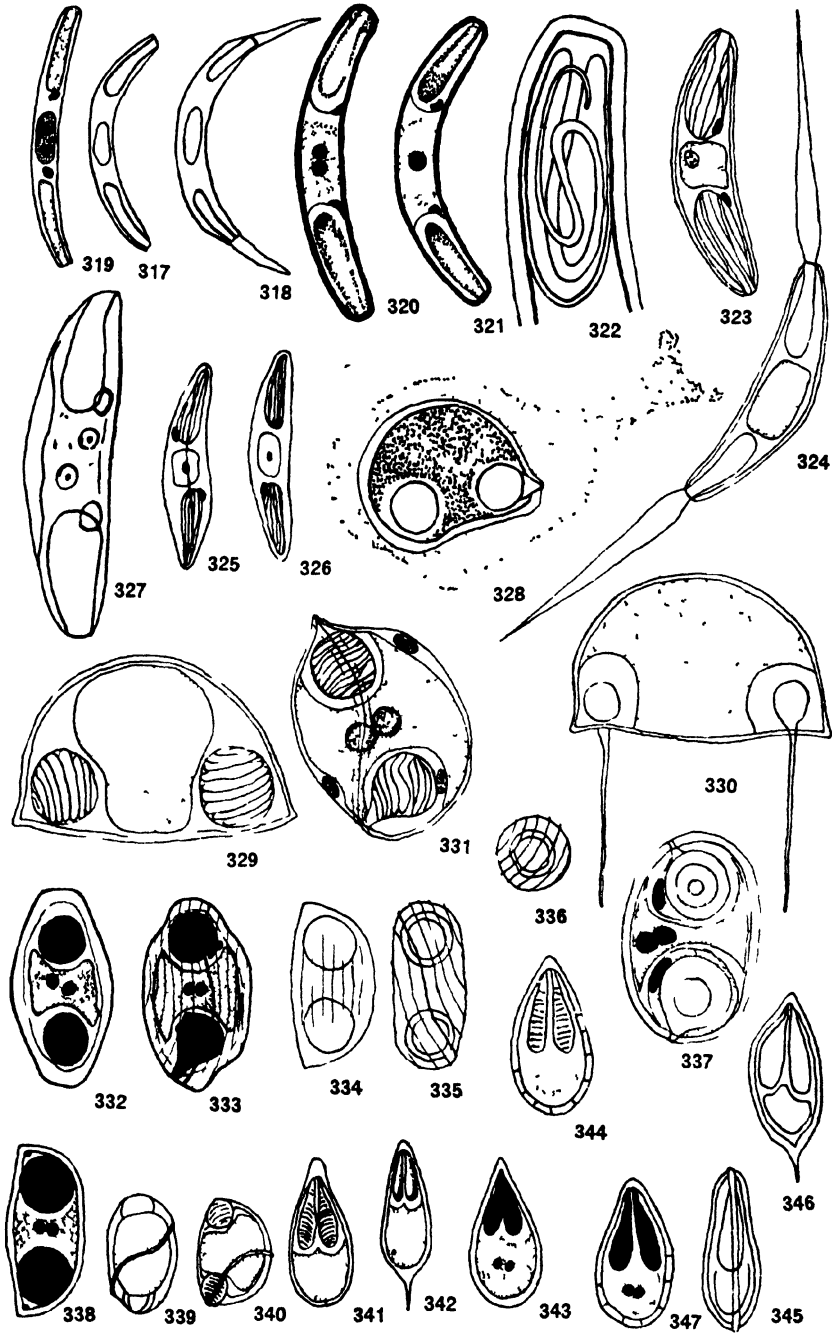




## PLATE XIV

## EXPLANATION OF PLATE

- Figs. 317 to 322. Spores of *Sphaeromyxa sabrazesi*.  
Figs. 317 to 319. After Laveran and Meanil (1900, Figs. 1, 3 and 4).  $\times 1500$ .  
Fig. 318. A spore treated with nitric acid (1900, Fig. 3).  
Figs. 320 and 321. Spores. After Schröder (1907, Figs. 39 and 41).  $\times 1500$ .  
Fig. 322. A polar capsule. After Schröder (1907, Fig. 45).  
Figs. 323 and 324. Spores of *Sphaeromyxa hellandi*. After Auerbach (1909, Fig. 5).  $\times$  about 1500.  
Figs. 325 and 326. Spores of *Sphaeromyxa ezneri*. After Awerinzew (1913a, Fig. 3).  $\times$  about 365.  
Fig. 327. A spore of *Sphaeromyxa gasterostei*. After Georgévitch (1916, Fig. 22).  
Figs. 328 to 331. *Zschokkella hildae*. After Auerbach (1910a and 1912).  
Fig. 328. A monosporous trophozoite (1912, Pl. 5, Fig. 2).  
Figs. 329 to 331. Spores (1910a, Fig. 62).  
Figs. 332 and 333. Spores of *Zschokkella nova*. After Klokacewa (1914, Fig. 2).  $\times$  about 2500.  
Figs. 334 to 338. Spores of *Zschokkella acheilognathi*. After Kudo (1916).  
Figs. 334 to 336. Different views of fresh spores (1916, Figs. 3d, 3e and 3f).  $\times 2250$ .  
Fig. 337. A young spore. Original.  $\times 2785$ .  
Fig. 338. A stained spore (1916, Fig. 3h).  $\times 2800$ .  
Figs. 339 and 340. Spores of *Zschokkella globulosa*. After Davis (1917, Figs. 135 and 134).  $\times 1500$ .  
Figs. 341 to 343. Spores of *Myxosoma dujardini*. After Thélohan (1895, Figs. 90, 91, and 89).  $\times 1500$ .  
Figs. 344 to 347. Spores of *Myxosoma funduli*. After Kudo (1918a, Fig. A).  $\times 1500$ .

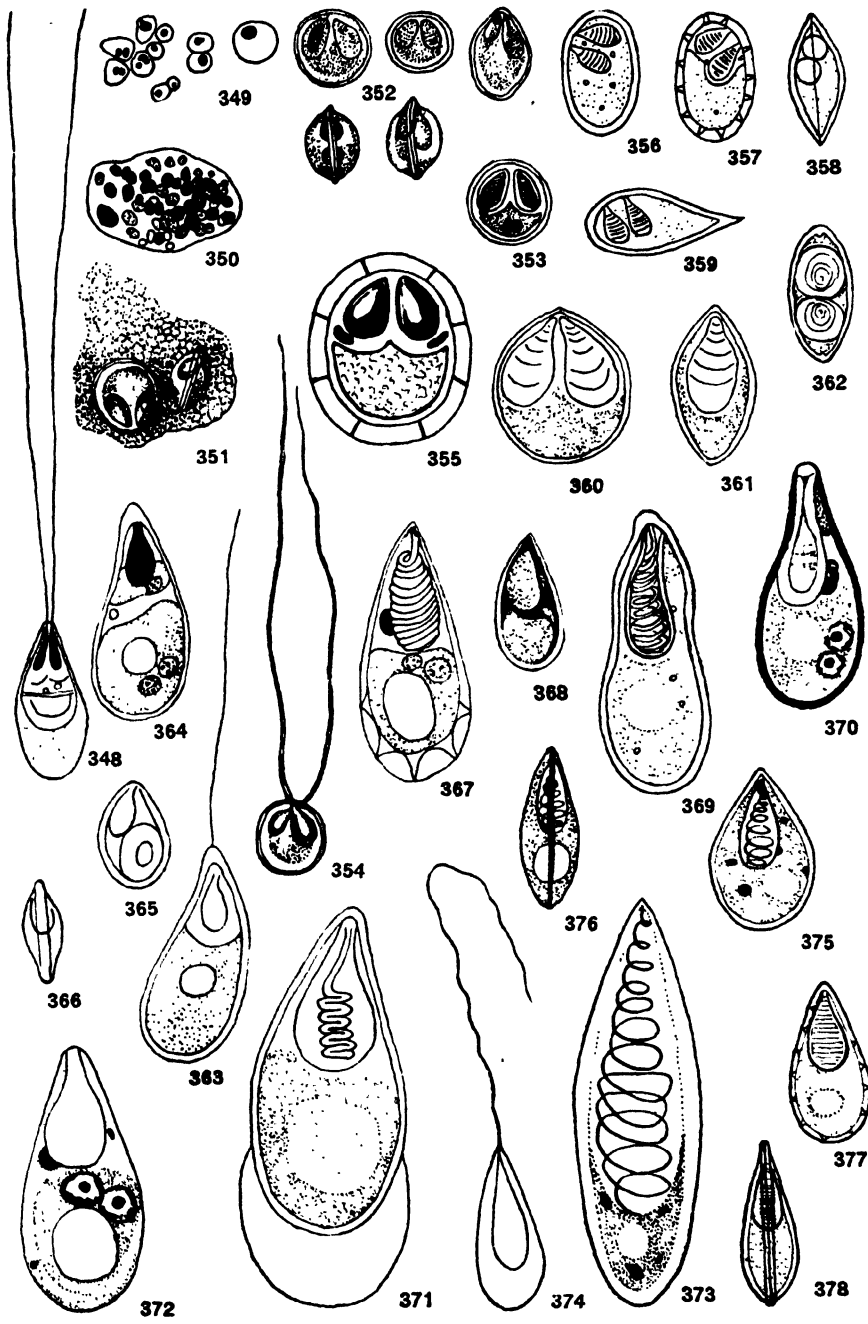




**PLATE XV**

## EXPLANATION OF PLATE

- Fig. 348. A spore of *Myxosoma*(?) *lobatum*. After Nemeczek (1911, Fig. 18).  $\times 1000$ .  
Fig. 349 to 354. *Lentospora cerebralis*. After Plehn (1905).  $\times 1200$ .  
Fig. 349. Various young ameboid forms; stained (1905, Textfig. 5).  
Fig. 350. A stained larger form (1905, Textfig. 5).  
Fig. 351. A trophozoite with two spores (1905, Textfig. 4).  
Fig. 352. Various spores (1905, Textfig. 2).  
Fig. 353. A stained spore (1905, Textfig. 3).  
Fig. 354. A spore with extruded polar filaments (1905, Textfig. 2).  
Fig. 355. A spore of *Lentospora multiplicata*. After Reuss (1906, Fig. 8).  $\times 1500$ .  
Figs. 356 to 359. Spores of *Lentospora asymmetrica*. After Parisi (1912, Fig. 7).  $\times$  about 1500.  
Figs. 360 to 362. Spores of *Lentospora acuta*. After Fujita (1912, Fig. 2).  $\times 2000$ .  
Figs. 363 and 364. Spores of *Myxobolus piriformis*. After Thélohan (1895, Figs. 117 and 116).  $\times 1500$ .  
Figs. 365 and 366. Spores of *Myxobolus unicusulatus*. After Müller (1841, Fig. 5).  
Fig. 367. A spore of *Myxobolus fuhrmanni*. After Auerbach (1909, Fig. 1b).  $\times 1840$ .  
Fig. 368. A spore of *Myxobolus oculi-leucisci*. After Trojan (1909, Fig. 3).  $\times 2000$ .  
Figs. 369 and 370. Spores of *Myxobolus toyamai*. After Kudo (Original and 1917, Fig. 40).  $\times 2500$ .  
Figs. 371 and 372. Spores of *Myxobolus notatus*. After Mavor (1916, Figs. 6C and 6B).  $\times 2600$ .  
Figs. 373 and 374. Spores of *Myxobolus rohita*. After Southwell and Prashad (1918, Figs. 26 and 27).  $\times$  about 1720 and 700 respectively.  
Figs. 375 and 376. Spores of *Myxobolus seni*. After Southwell and Prashad (1918, Figs. 29 and 30).  $\times$  about 1700.  
Figs. 377 and 378. Spores of *Myxobolus misgurni*. Original.  $\times 1500$ .



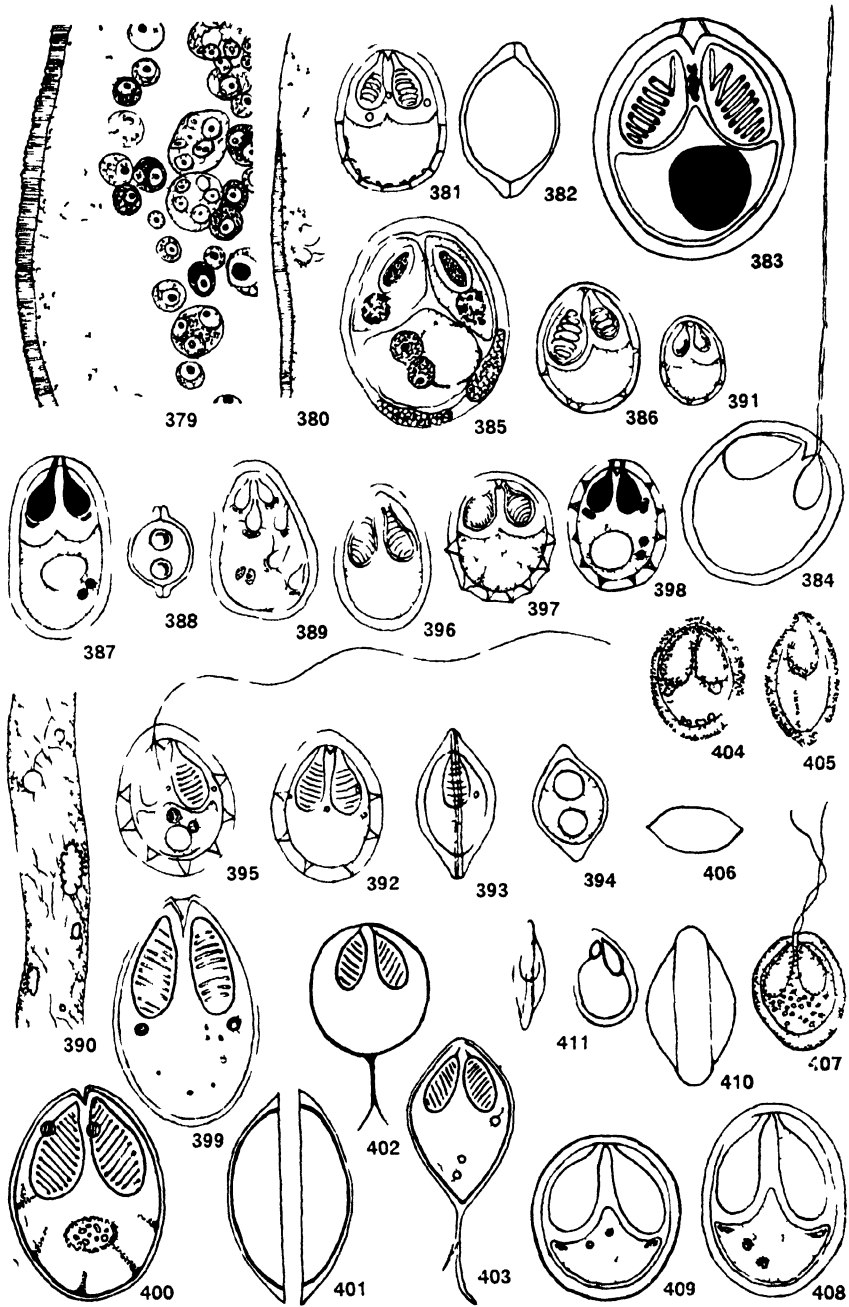




## PLATE XVI

## EXPLANATION OF PLATES

- Figs. 379 to 385. *Myxobolus Pfeifferi*.  
Figs. 379 and 380. Parts of section thru cyst. After Keysseltz (1908a, Pl. 15, Figs. 1 and 2).  
Fig. 381. A spore. After Thélohan (1895, Fig. 77).  $\times 1500$ .  
Fig. 382. An optical section of spore. After Keysseltz (1908a, Fig. A).  
Fig. 383. A spore treated with Lugol's solution. After Keysseltz (1908a, Pl. 14: Fig. 92).  
Fig. 384. A spore with extruded filaments. After Keysseltz (1908a, Fig. C).  
Fig. 385. A stained young spore. After Keysseltz (1908a, Pl. 14, Fig. 81).  
Fig. 386. A spore of *Myxobolus dispar*. After Thélohan (1895, Fig. 86).  $\times$  about 1500.  
Figs. 387 to 389. Spores of *Myxobolus ellipsoides*. Fig. 389. An abnormal spore with six polar capsules. After Thélohan (1895, Figs. 112, 113 and 115).  
Fig. 390. A part of the infected intestine of *Mugil auratus*, showing cysts of *Myxobolus exiguus*. After Parisi (1912, Fig. 9e).  $\times$  about 3.  
Fig. 391. A spore of *Myxobolus exiguus*. After Thélohan (1895, Fig. 98).  $\times 1500$ .  
Figs. 392 to 395. Spores of *Myxobolus exiguus*. After Parisi (1912, Fig. 9).  $\times 2500$ .  
Fig. 396. A spore of *Myxobolus oviformis*. After Thélohan (1895, Fig. 81).  $\times 1500$ .  
Figs. 397 to 398. Spores of *Myxobolus mülleri*. After Thélohan (1895, Figs. 96 and 97).  $\times 1500$ .  
Figs. 399 and 400. Spores of *Myxobolus mülleri*. After Bütschli (1881, Figs. 1 and 2).  
Fig. 401. A spore of *Myxobolus mülleri* in conc. sulphuric acid. After Bütschli (1881, Fig. 6).  
Figs. 402 and 403. Abnormal spores of *Myxobolus mülleri*. After Bütschli (1881, Figs. 9 and 8).  
Figs. 404 and 405. Spores of *Myxobolus lintoni*. After Linton (1891, Figs. 3 and 5).  
Fig. 406. Diagram of the cross section of a spore of *Myxobolus lintoni*. After Linton (1891, Fig. 8).  
Fig. 407. A spore of *Myxobolus lintoni* with extruded polar filaments. After Linton (1891, Fig. 10).  
Fig. 408. A stained spore of *Myxobolus lintoni*. After Gurley (1894, Pl. 26, Fig. 7).  $\times$  about 2000.  
Figs. 409 and 410. Spores of *Myxobolus globosus*. After Gurley (1894, Pl. 26, Fig. 7).  $\times$  about 2900.  
Fig. 411. Spores of *Myxobolus inaequalis*. After Müller (1841, Fig. 6).

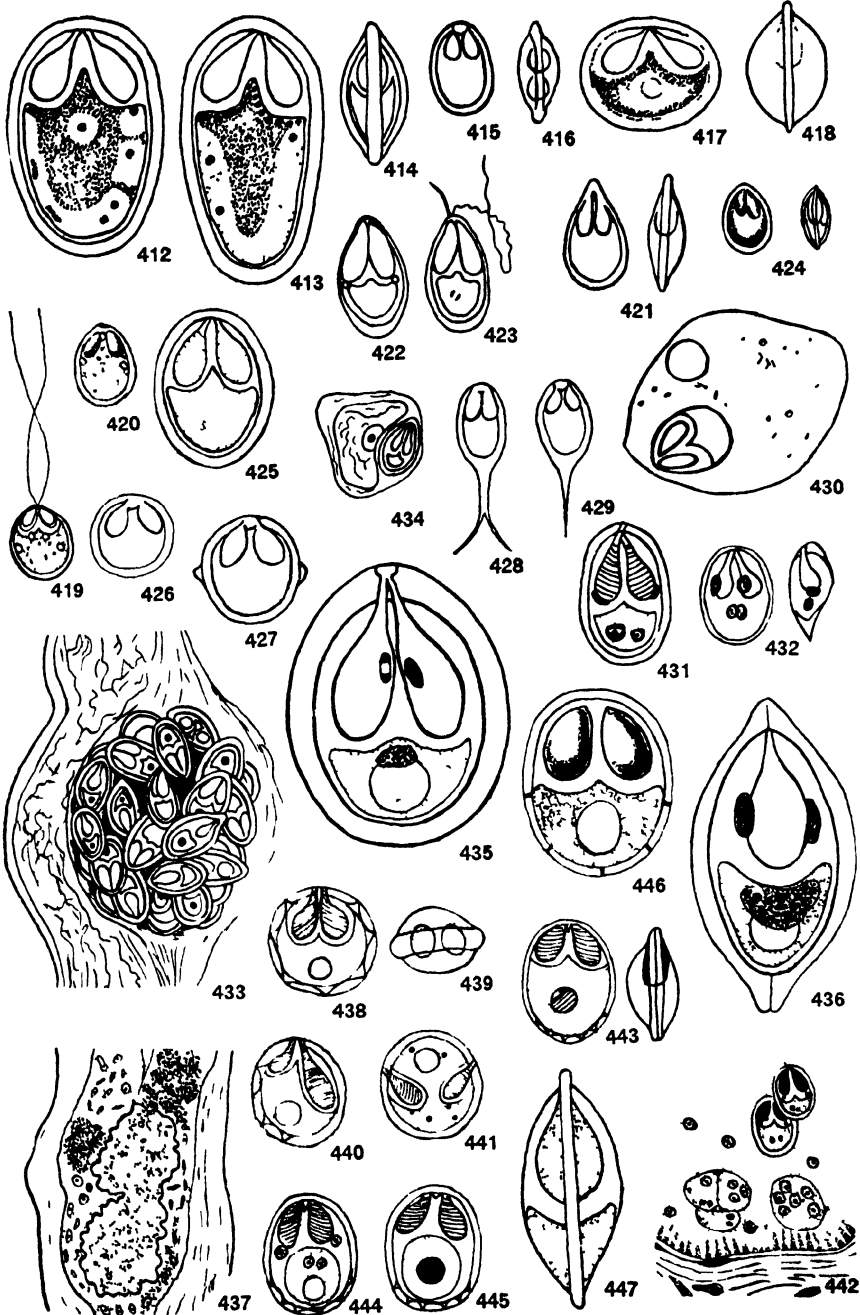




## PLATE XVII

## EXPLANATION OF PLATE

- Figs. 412 to 416. Spores of *Myxobolus oblongus*. Figs. 412 to 414. After Gurley (1894, Pl. 26, Fig. 6).  $\times 2300$ . Figs. 415 and 416. After Müller (1841, Fig. 9).
- Figs. 417 and 418. Spores of *Myxobolus transovalis*. After Gurley (1894, Pl. 29, Fig. 1).
- Figs. 419 and 420. Spores of *Myxobolus obesus*. After Balbiani (1884, Fig. 39).
- Fig. 421. Spores of *Myxobolus cycloides*. After Müller (1841, Fig. 3).
- Figs. 422 and 423. Spores of *Myxobolus anurus*. After Cohn (1895, Fig. 25).  $\times 1500$ .
- Fig. 424. Spores of *Myxobolus* sp.  $\times 700$ . After Bütschli (1882, Pl. 36, Fig. 23).
- Fig. 425. *Myxobolus* sp. After Gurley (1894, Pl. 28: Fig. 4a).  $\times$  about 1500.
- Figs. 426 to 429. Spores of *Myxobolus* sp. After Müller (1841, Fig. 4).
- Fig. 430. A vegetative form of *Myxobolus cyprini*. After Doflein (1898, Fig. 112).
- Figs. 431 and 432. Spores of *Myxobolus cyprini*. After Doflein (1898, Figs. 113 to 115).
- Figs. 433 to 436. *Myxobolus neurobius*. After Schuberg and Schröder (1905).
- Figs. 433 and 434. Longitudinal and transverse sections thru infected nerve fibres (1905, Figs. 2 and 4a).  $\times 520$ .
- Figs. 435 and 436. Spores (1905, Figs. 5 and 6). Comp. oc. 12 and imm. obj. 2mm.
- Figs. 437 to 441. *Myxobolus aeglefini*. After Auerbach (1906a).
- Fig. 437. A cyst in the sclerotic cartilage of the eye of *Gadus aeglefini* (1906a, Fig. 2).
- Figs. 438 and 439. Spores (1906a, Figs. 5a and 3d).  $\times$  about 1320.
- Figs. 440 and 441. Abnormal spores (1906a, Figs. 5b and 5c).  $\times$  about 1320.
- Figs. 442 to 445. *Myxobolus gigas*. After Auerbach (1906b).
- Fig. 442. A part of the section of a cyst (1906b, Fig. 1).
- Figs. 443 to 445. Spores (1906b, Figs. 3a, 3c, 5 and 3b).  $\times$  about 850.
- Figs. 446 and 447. Spores of *Myxobolus volgensis*. After Reuss (1906, Fig. 1).  $\times 2000$ .



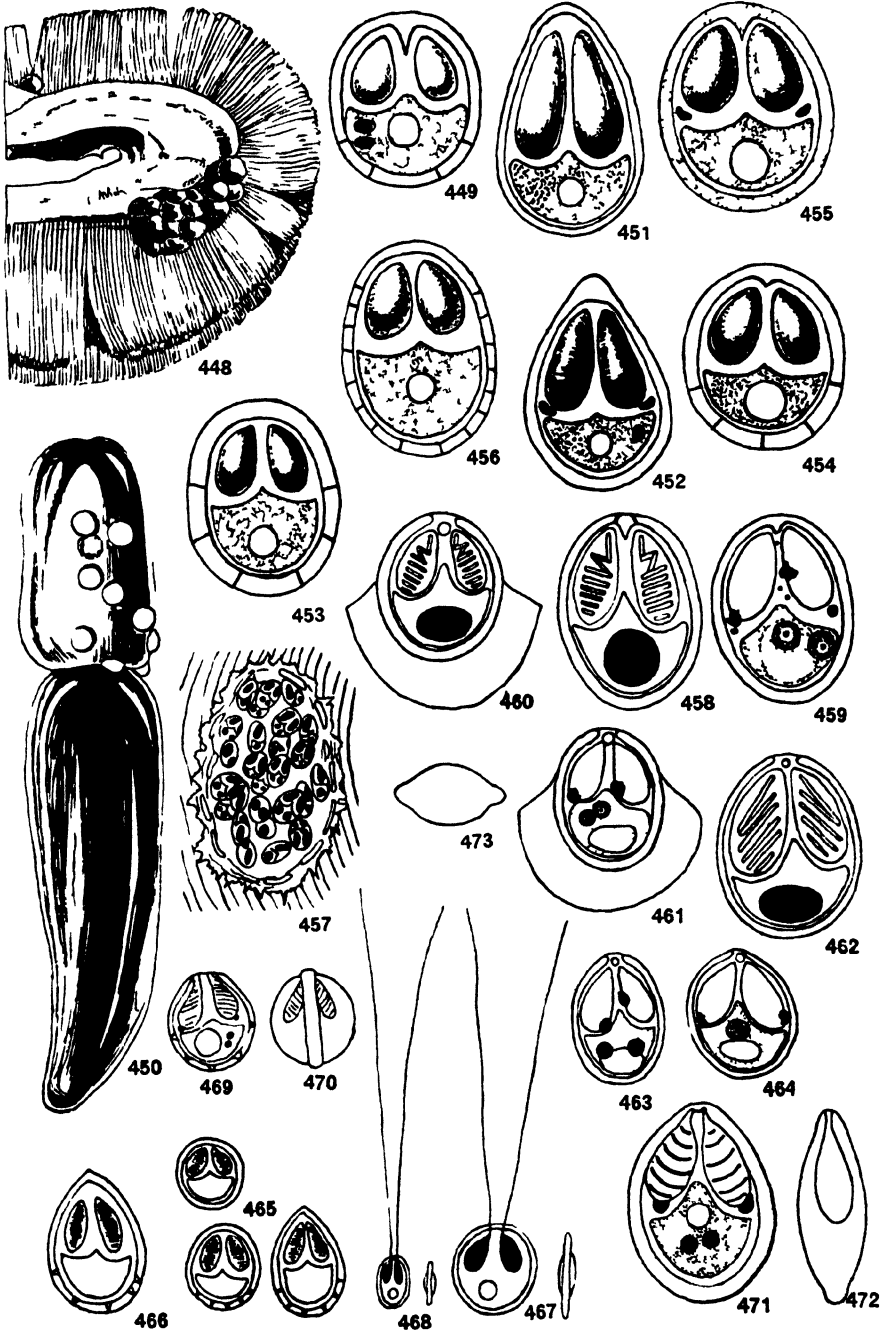




**PLATE XVIII**

## EXPLANATION OF PLATE

- Fig. 448. The branchia of *Lucioperca volgensis* with cysts of *Myxobolus volgensis*. After Reuss (1906, Fig. 2).  $\times 2.25$ .
- Fig. 449. A spore of *Myxobolus scardinius*. After Reuss (1906, Fig. 3).  $\times 1500$ .
- Fig. 450. Air bladder of *Scardinius erythrophthalmus* with the cysts of *Myxobolus physophilus*. After Reuss (1906, Fig. 5).  $\times 2$ .
- Fig. 451. A spore of *Myxobolus physophilus*. After Reuss (1906, Fig. 4).  $\times 1500$ .
- Fig. 452. A spore of *Myxobolus macrocapsularis*. After Reuss (1906, Fig. 6).  $\times 1500$ .
- Fig. 453. A spore of *Myxobolus sandrae*. After Reuss (1906, Fig. 7).  $\times 2000$ .
- Fig. 454. A spore of *Myxobolus bramae*. After Reuss (1906, Fig. 9).  $\times 1500$ .
- Fig. 455. A spore of *Myxobolus balleri*. After Reuss (1906, Fig. 10).  $\times 1500$ .
- Fig. 456. A spore of *Myxobolus cyprinicola*. After Reuss (1906, Fig. 11).  $\times 1500$ .
- Figs. 457-459. *Myxobolus squamae*. After Keysseltz (1908a).
- Fig. 457. A part of the infected scale (1908a, Fig. G.)
- Fig. 458. A spore treated with Lugol's solution (1908a, Pl. 14, Fig. 94).
- Fig. 459. A stained spore (1908a, Pl. 14, Fig. 96).
- Figs. 460 and 461. Spores of *Myxobolus cordis*. After Keysseltz (1908a).
- Fig. 460. A spore treated with Lugol's solution (1908a, Pl. 16, Fig. 16).
- Fig. 461. A strained spore (1908a, Fig. B on page 281).
- Figs. 462 to 464. Spores of *Myxobolus musculi*. After Keysseltz (1908a).
- Fig. 462. A spore treated with Lugol's solution (1908a, Pl. 15, Fig. 13).
- Fig. 463 and 464. Stained spores (1908a, Figs. D and E on page 286).
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- Fig. 467. Spores of *Myxobolus rotundus*. After Nemeczek (1911, Figs. 10 and 11).  $\times 1000$ .
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**PLATE XIX**

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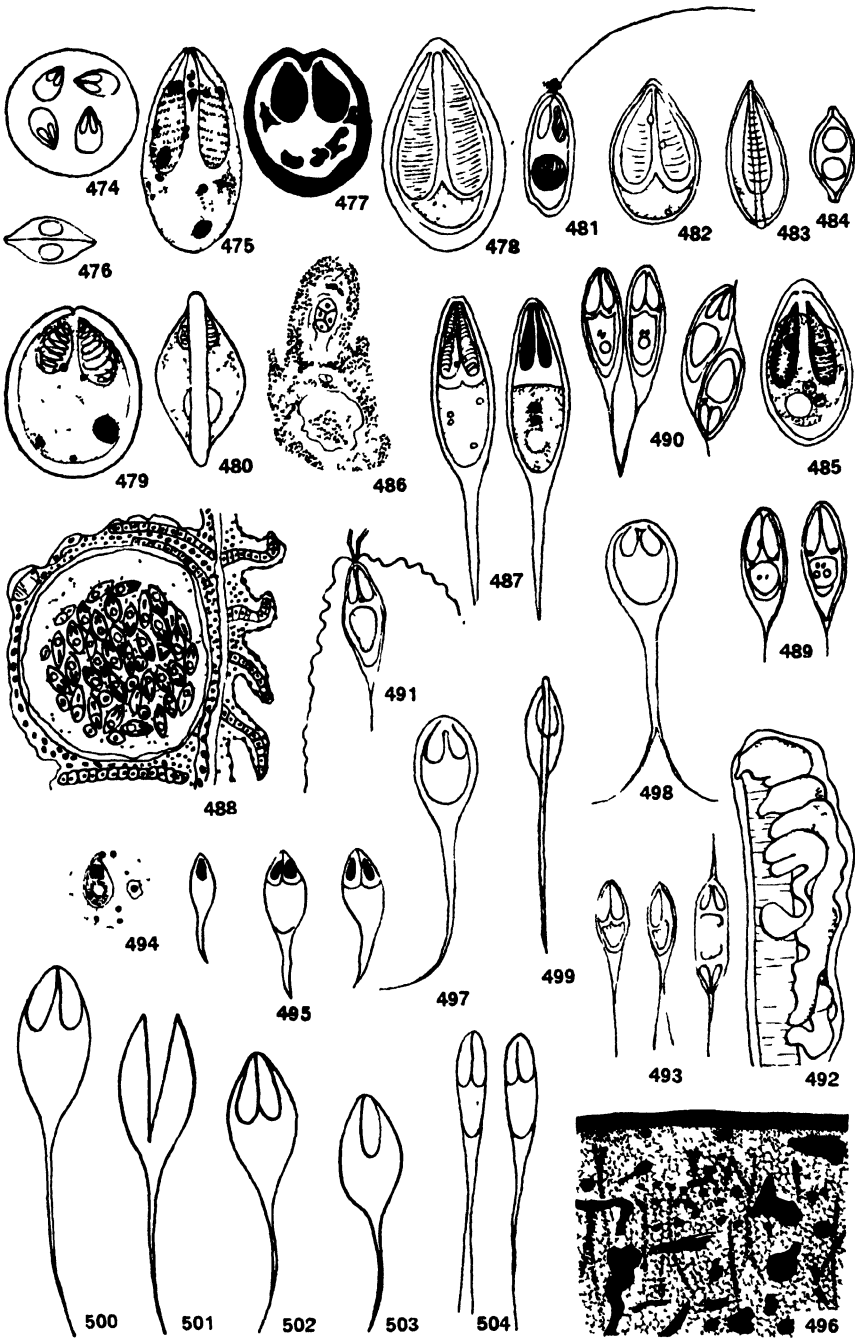
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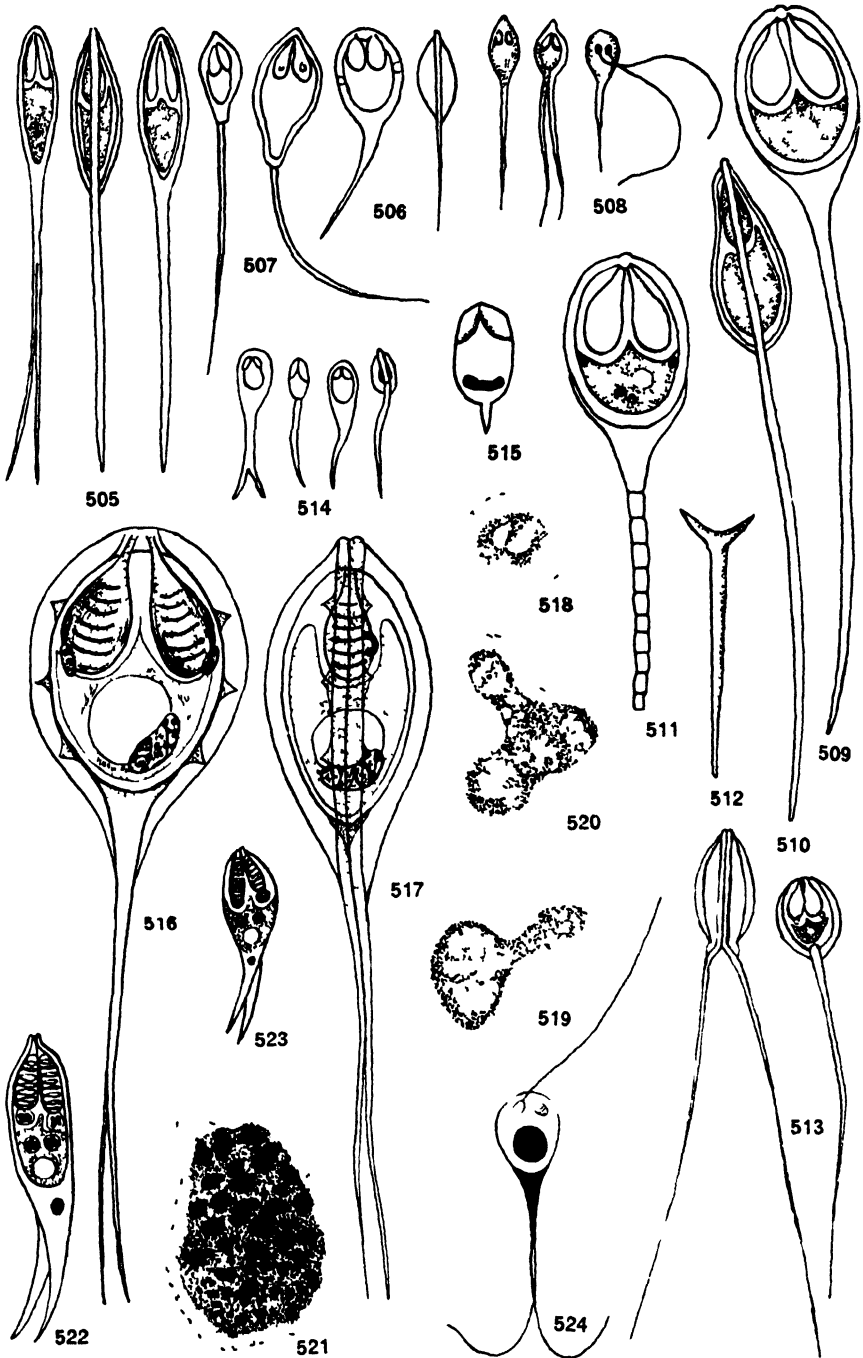




## PLATE XX

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- Fig. 505. Spores of *Henneguya Gurleyi*. After Gurley (1894, Pl. 33, Figs. 8c, 6 and 7).  
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- Fig. 506. Spores of *Henneguya strongylura*. After Müller (1841, Fig. 2).
- Fig. 507. Spores of *Henneguya monura*. After Ryder (1880, Figs. 1c and 2d).
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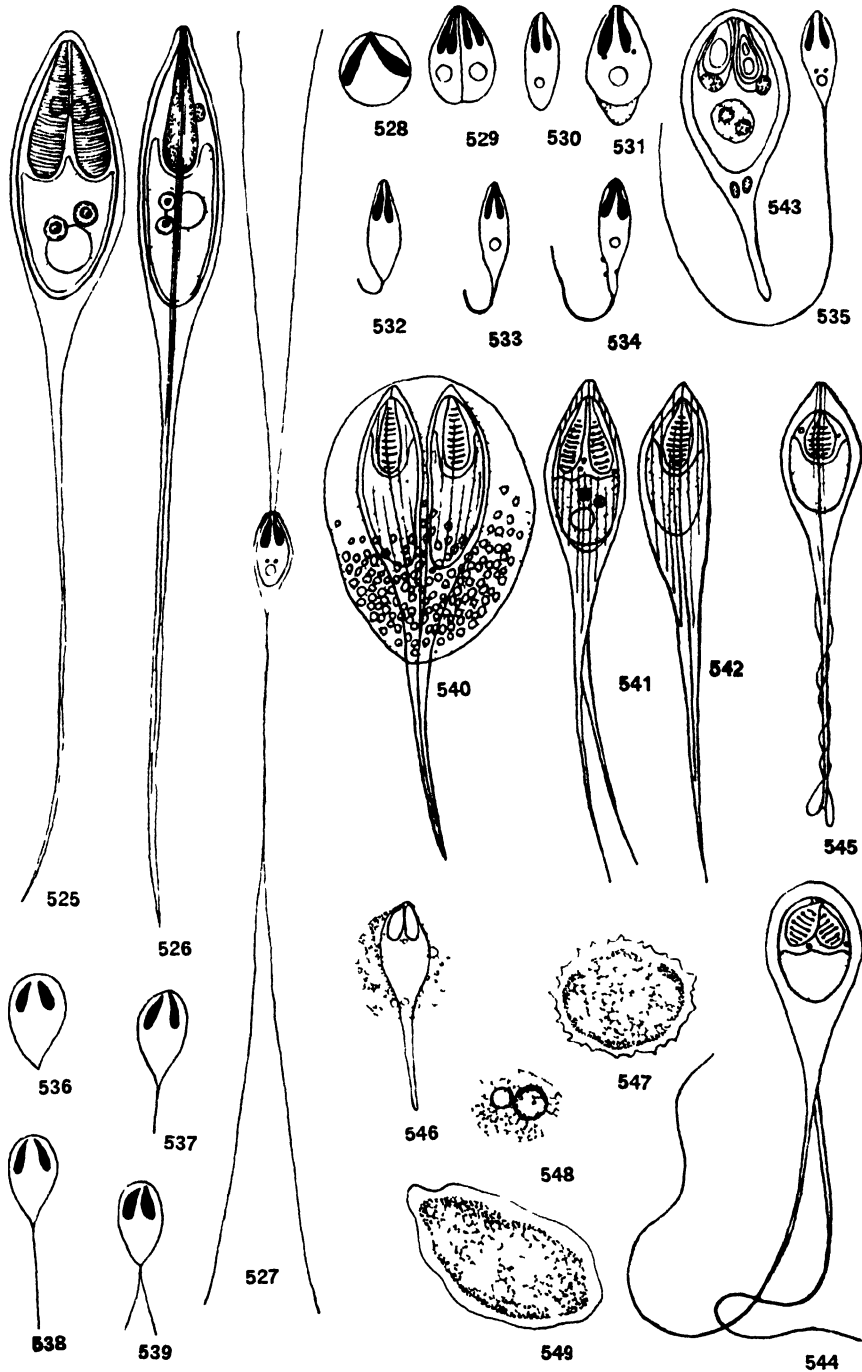




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## PLATE XXII

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Fig. 564. Front view of a preserved and decolorized spore.

Fig. 565. The same views of two spores restained with Giemsa's mixture.

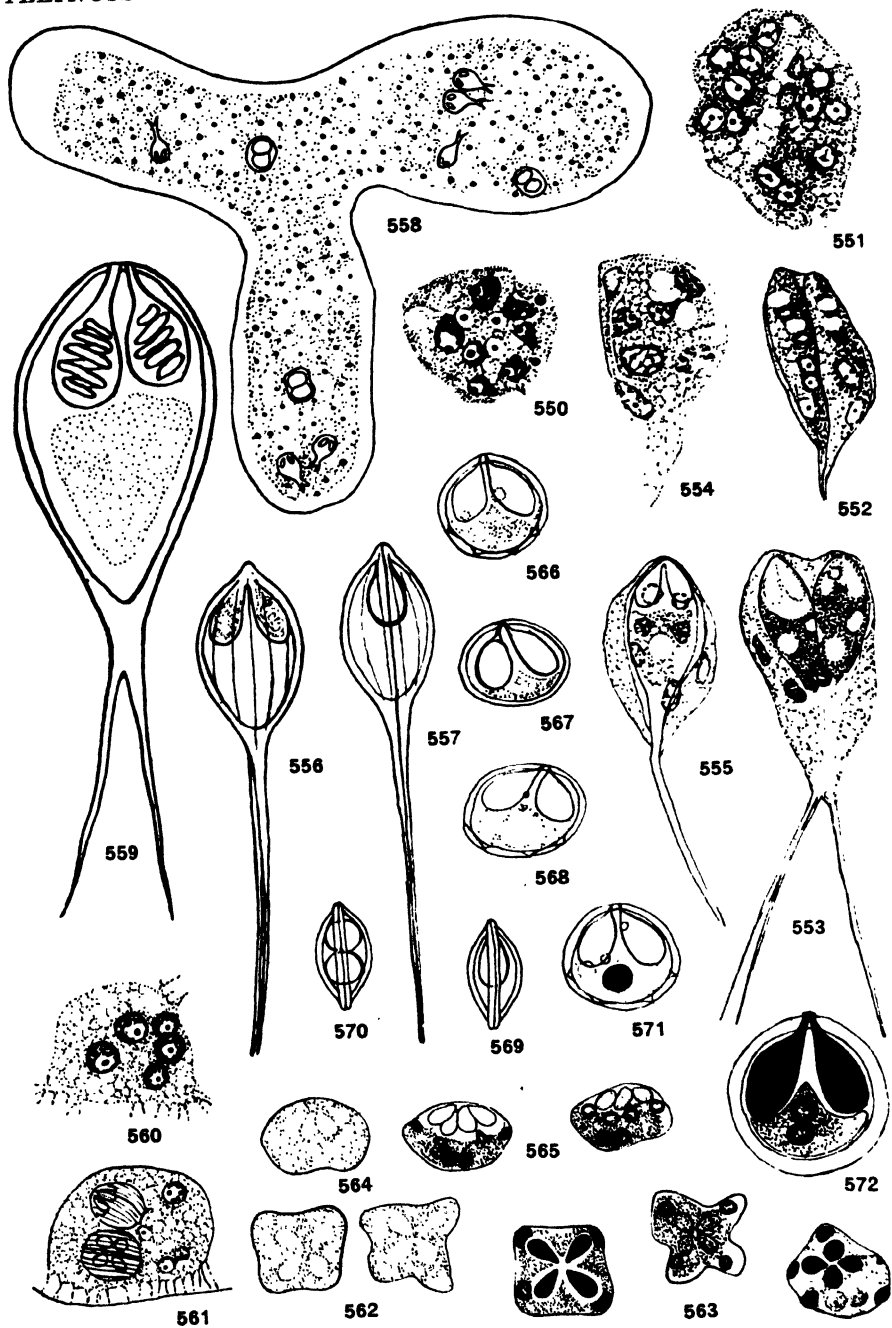
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**PLATE XXIII**

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Fig. 587. A trophozoite (1915, Fig. 6).

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Fig. 586. A trophozoite with attached *Ceratomyxa acadiensis* (1915, Fig. 8).  $\times 830$ .

Fig. 587. A trophozoite (1915, Fig. 6).

Figs. 588 and 589. Trophozoites of genus et species incertae. After Mavor (1916a, Figs. 3d and 3b).  $\times 660$ .

Fig. 590. Spores of genus et species incertae. After Linton (1891a, Fig. 2).

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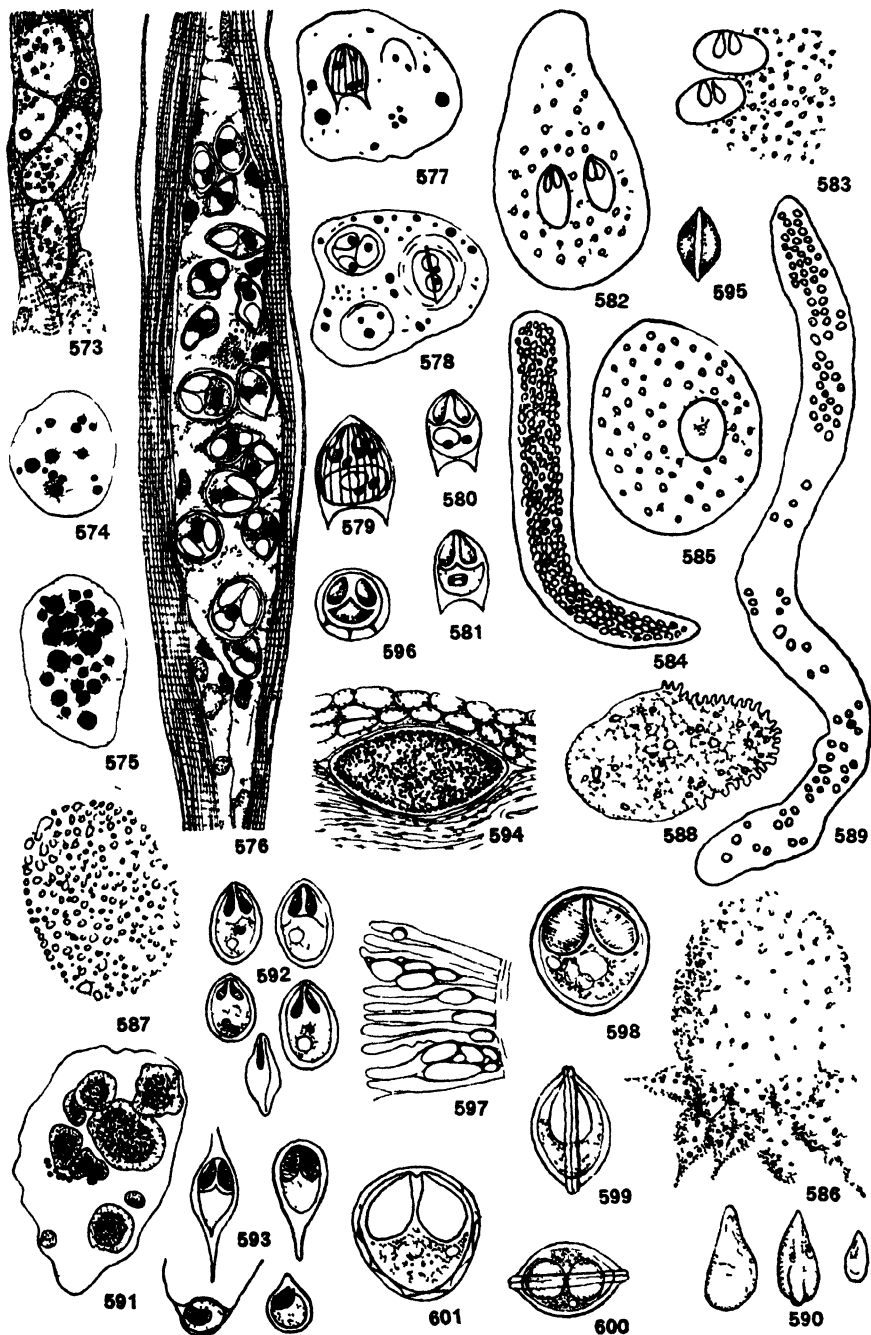
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**PLATE XXIV**

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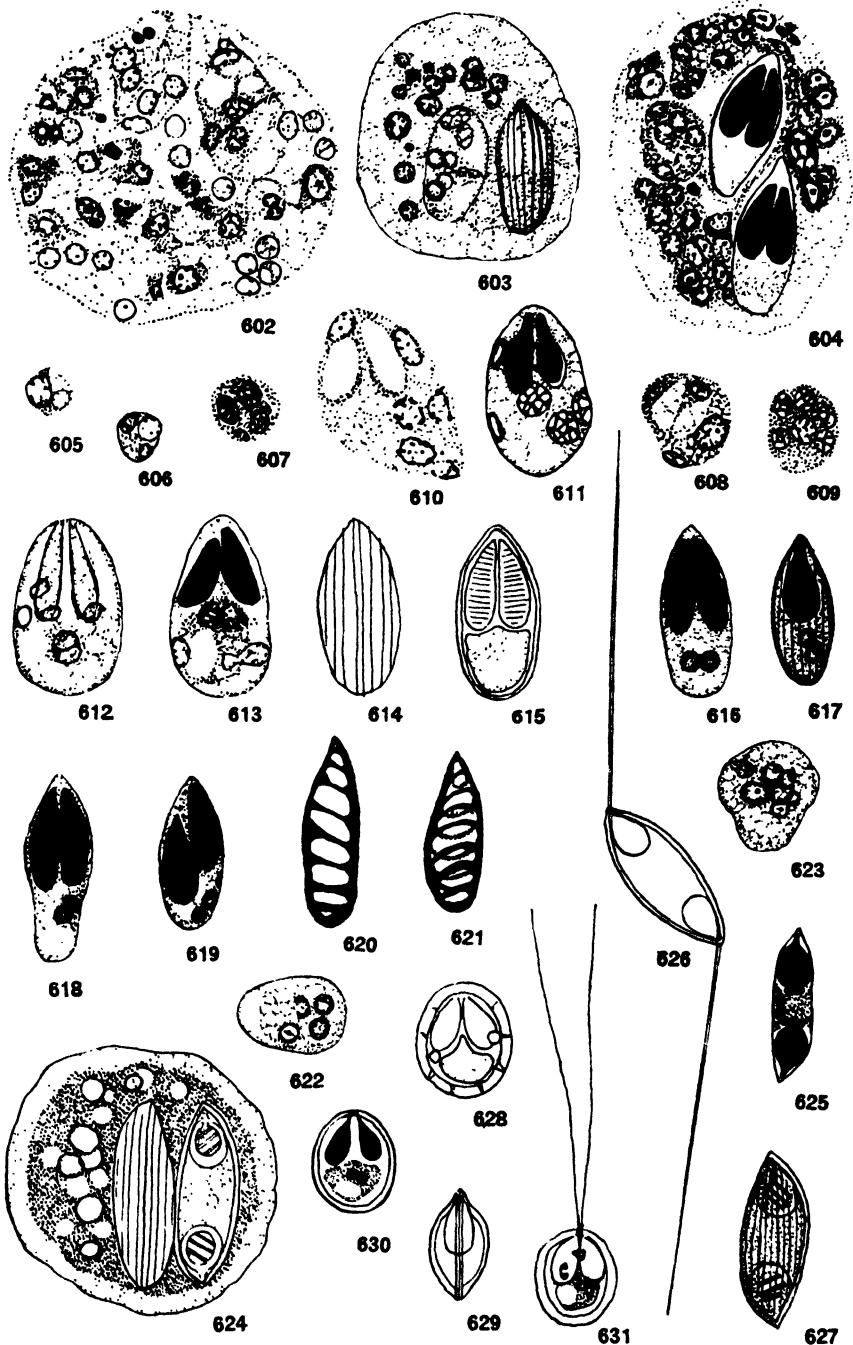
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## PLATE XXV

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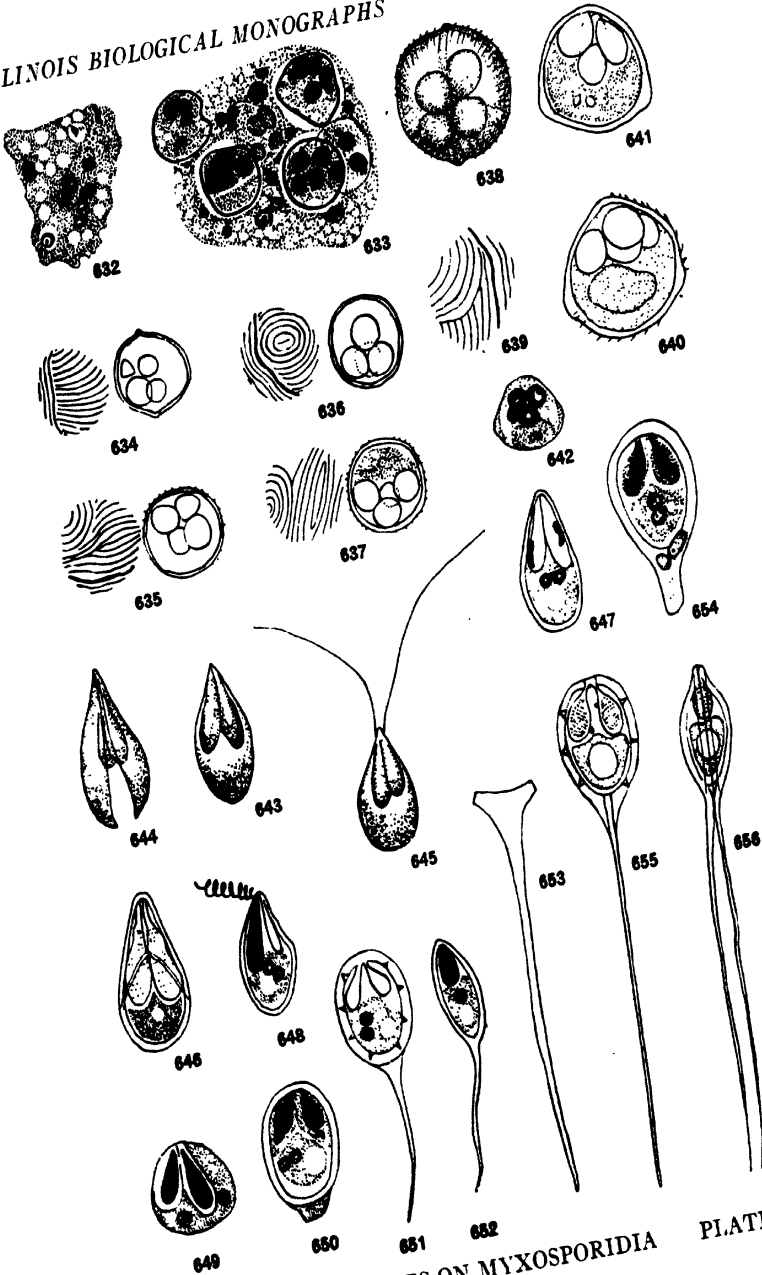
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